Systematic Zoology

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The Problem of Intraspecific Variation in Parasitic Animals

THIS SYMPOSIUM, sponsored jointly by the Society of Systematic Zoology, the American Microscopical Society, and the American Society of Parasitologists, and arranged by John S. Rankin, Jr., was held on August 27, 1956 at Storrs, Connecticut.

Participants

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Parasitic Nematodes	•	M. B. CHITWOOD
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Intraspecific Variation in Parasitic Protozoa

REGINALD D. MANWELL

I BELIEVE it was the late Dr. N. A. Cobb who once told a group of graduate students, of whom I was one, that it should be a part of the doctoral requirements for each candidate to describe at least one new species. What he had in mind, I am sure, was not simply the discovery of more kinds of living things, nor even the training of biologists versatile enough to act as taxonomists if required, but development of the knowledge and skills essential to good classification. I doubt that anyone who has not attempted an exercise of this sort realizes all that is involved: a thorough knowledge of the morphology and life-history of the group concerned, an appreciation of the importance of host-parasite physiology, and an acquaintance with the literature—at the very least.

In addition to all this, however, taxonomists today are confronted with difficulties arising from what has been termed, in the title of this symposium, "intraspecific variation." Not that the earlier taxonomists were unaware of such variation, but the concept of living things as divisible into fixed species was much more strongly held than it is today. Parasitologists shared this conviction, and they added to it a belief in a rather rigid host-parasite specificity, so that often merely finding a given form of parasite in a new host species was reason enough for calling the former a new species.

Today even the concept of species as an entity is under attack by some geneticists. After listening to one of them talk on *Neurospora* genetics not very long ago, I asked him whether the experimental development of new strains and the discovery of the genetic mechanisms involved did not make the whole concept of species very misty, at least in the case of these relatively simple organisms. His reply was that he did not know whether it did or not; the question seemed to him of small importance. Yet to those who study living things of any kind, and certainly to parasitologists interested in research on the protozoa, taxonomy is an indispensable science. We must somehow be able to define just what we are working with.

Certainly the problem of the taxonomist dealing with the Protista is a difficult one. The conventional definition of a species as "a group of animals that mate with one another and that resemble one another more than they do individuals in other groups of animals" (Hegner's *College Zoology,* 1942), or "Species are groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups" (Mayr *et al,* 1953) scarcely applies at this level. That such definitions of species, even for the higher animals, are not very satisfactory is recognized by most biologists, but, as remarked by Hunter and Hunter (1949), the species concept is "difficult to define but universally used."

The Species in Parasitic Protozoa

If we are concerned with the parasitic Protista, the problem becomes even more troublesome. Though Mayr (1942) had the Insecta especially in mind when he remarked "The taxonomy of parasites is therefore a particularly difficult field," we can be sure that he would have conceded it to be equally true of the Protozoa.

This is so for a number of reasons: Among them is the very considerable amount of variation which often exists even in what seems to be an unmixed strain, the relative lack of a strict host-parasite specificity in many cases, our ignorance of those biochemical peculiari-

ties of the parasite (certainly as important as its morphological characteristics) which determine its behavior in the host, and, of course, our inability to use that first requirement that members of a given species be able to "mate with one another" but not with members of other species.

Even more fundamental, perhaps, is the lack of agreement among parasitologists and protozoologists, in many cases, as to just what constitutes a species. To say, as we might do, that a species is a group of organisms, parasitizing one or a number of host species in more or less similar fashion, sharing a similar environment and similar in life-history, and morphologically very much alike, would only be to describe our present practice. But it would ignore many difficulties. One of them is how much variation there can be within what we call a species before we consider the possibility that it should be subdivided into varieties, or into subspecies, or even into two or more species. Here, of course, there is no more agreement as to just how subspecies, varieties, and races should be defined.

Essentially, the problem is a genetic one, but genetically controlled characters can seldom be considered by themselves; the environment (the host) probably always plays a role.

The importance of the host in influencing the behavior and morphology of parasites is well known to parasitologists. It is only necessary to mention the manner in which the host species may determine the rate of egg production in some helminths, or the changes induced in the morphology of certain of the species of avian malaria parasites when introduced into another host species [e.g. in *Plasmodium relictum* when transferred from the canary to the chicken (Manwell, 1943)]. Similarly, some species of avian malaria exhibit exoerythrocytic stages only in certain species of hosts. But we still know almost nothing about the extent to which host-induced variations occur in nature.

Determining Specific Limits

These difficulties are well illustrated by the two closely related genera of blood parasites, *Haemoproteus* and *Leucocytozoon*. The former is extremely common in birds and is also found in some reptiles. The latter genus is restricted to birds, in which it is equally common. Both genera are of special interest, because of their kinship to the malaria parasites.

These two genera were created in 1890, and they have been rather extensively studied in the nearly seventy years since. Numerous species of both have been described, most of them based chiefly on an assumed host-parasite specificity. Yet the gametocytes (which are all we ordinarily see), in each of the genera, are often so similar in morphology as to be virtually indistinguishable, and there is little experimental evidence, thus far, of strict host-parasite specificity (although it may well exist). Probably species of both genera should be defined chiefly in terms of life-history, vectors and the like, but until much basic research can be done there is not likely to be much agreement in either case on just what constitutes a species.

The instance just discussed is an illustration of the difficulty of knowing what a species is. There is fair agreement among malariologists as to how a species of *Plasmodium* should be defined [although even here some difference of opinion still exists, as the late Colonel Sinton made clear in a recent article (Sinton, 1955)]; but the case of *Plasmodium circumflexum*, a common malaria parasite of birds, is an instance of the difficulties posed by intraspecific variation. This is a species quite easily distinguishable from any other, since its morphology is characteristic. Some years ago, however, we were able to secure six strains of different host and geographical origin, and several of them, although identical in morphology, produced quite different immunological reactions in experimentally infected canaries. More recently, we attempted to establish laboratory infections of this species in the duck, and with one strain we succeeded very well. A number of other strains, however, produced either extremely light and transitory infections or none at all. Rapid passage, the use of

large numbers of ducklings (to minimize the effect of individual host variations in resistance), and splenectomy either just prior to or immediately after parasite inoculation, all failed to result in adaptation of any of these strains to this host. It is therefore apparent that, whatever the physiological peculiarities of the parasites are that determine their ability to live in a given host species, they must often be highly stable. Should we, then, use them as bases for the creation of new species, as we do differences in morphology? Or for subspecies? Or should we simply label them as "strains," (as we do)?

In other cases, however, there is a very considerable ability on the part of the parasite to adapt to a new host, as with, at least, certain strains of *Plasmodium hexamerium*. Our first attempts to infect ducklings with this parasite were a complete failure, but later experiments with other strains were successful, and now we are regularly producing much heavier infections in this host than are ever observed in the passerine species in which *Plasmodium hexamerium* naturally occurs. Much greater versatility with regard to host species occurs with *Toxoplasma gondii* (although this parasite may not be a protozoan). A strain isolated from the crow produced, at first, very light infections in that very susceptible host, the white mouse, and showed a somewhat different predilection for certain organs, but with repeated passage its behavior became increasingly like that of strains of the same parasite of mammalian origin. There must be few species of parasites which occur naturally in as large a variety of host species, and in species which have so broad a taxonomic spectrum.

From some points of view morphological variation is even more troublesome. It is well illustrated by the two species of avian malaria parasite, *Plasmodium relictum* and *P. cathemerium*. These species were doubtless both observed by early students of the blood parasites of birds, but they were not differentiated until Hartman's work in 1927, and the question of proper nomenclature remained unsettled for several years longer. In this case, separation into distinct species was based chiefly on the shape of pigment granules in the gametocytes, and differences in the length of the asexual cycle. Yet, even though the validity of both species is generally recognized, many investigators of avian blood parasites still prefer to lump them together in survey reports, simply because there is so much variation. Herman *et al.* (1954) remarked on the "different strain types" observed in naturally occurring *Plasmodium relictum* malaria in English sparrows, morphological differences including variations in shape and size of pigment granules, in size of gametocytes, and in the range and mean number of merozoites per segmenter.

It must, of course, be remembered that the malaria parasites, like all forms in which sexual reproduction occurs, undoubtedly exist as almost infinitely varying, genetically distinct strains. Except in the very rare cases of infection derived from parasites originating from a single oocyst, really pure strains do not exist in nature. Although most mosquito infections are probably contracted from feeding on a single case, mixed infections are so common among susceptible birds and mammals that hybridization of different species of *Plasmodium* in the mosquito is always a possibility. This is a problem so far almost unstudied, as far as I know. If such hybridization occurs in the numerous sporozoan infections in which it seems possible, what becomes of our concept of species among such parasites, based as it is almost wholly on morphology?

Types of Intraspecific Variation

Presumably, "intraspecific variation" embraces a number of quite distinct phenomena. The earliest one to be recognized must have been the kind of variability seen in all living things, and exemplified by such individual differences among parasites as those of size, reaction to stains, and (often) the number of merozites produced by segmenting cells. How

great a problem this may be is emphasized by the author of a recent paper on trichomonads, when he remarks on the difficulty of a conventional description of species because of the "extreme pleiomorphism" of his parasite. Corresponding physiological variations also occur among strains of *Trichomonas gallinae* of varying origin. Some kill pigeons very quickly, whereas others tend to produce relatively chronic and benign infections (Stabler, 1954). This trichomonas also shows a rather remarkable degree of host adaptability, for it not only occurs naturally in a number of avian species, but it also is quite capable of producing infection in some mammals (e.g., the white mouse) when experimentally introduced.

Another group of parasitic protozoa in which there is great variability, both in morphology and in the character of infections produced, are the trypanosomes, although it is possible that this variability may be in part due to stages in the life-cycles, which are very incompletely known. Such pleiomorphism is especially marked in the trypanosomes of birds, and it may also be remarked that perhaps in no other group of these parasites is our knowledge more fragmentary.

It is a familiar fact that variant forms within a species when carefully studied have often been analysable into races, as in the case of *Endamoeba histolytica*, first shown to consist of such races by Dobell and Jepps (1918). Here size variation is apparently often correlated with variation in pathogenicity also. Subspecies and races are at best difficult to define, and particularly so when the terms are applied to Protozoa. It is clear that we can hardly use Mayr's criterion of *geographical* isolation for a subspecies when this term is applied to a parasitic protozoan.* It seems likely that the solution to this problem will remain an individual one on the part of the parasitologist. It is important to remember, however, that differences in a parasite population which might seem to justify division into races or subspecies may sometimes be host-induced, and laboratory study may be necessary to settle the matter. Here again we must use caution, for there are only a relatively few species of animals that can be successfully maintained in the laboratory and used as experimental hosts, and fewer still susceptible to infection with a given species of parasite. It can therefore seldom be assumed that the behavior of the latter in a laboratory host is necessarily like that in the natural host. But if two strains of parasite exhibit noticeable and consistent differences when studied in the same host species, we can at least know that we are dealing with real dissimilarities even though we may still be uncertain whether they should be accorded taxonomic value.

So far we have said nothing of intraspecific variation resulting from parasite mutations. In a sense, perhaps any variation must be regarded as originally due to mutation. But it is surprising that (to my knowledge, at least) no natural or artificially induced mutations have been reported for the parasitic protozoa. Of course they occur, and a careful study of this problem should lead to some interesting results.

Perhaps what we most need is a realization on the part of all parasitologists who feel the urge to describe new species or subspecies of parasitic protozoa that any taxonomic unit, small or large, is a genetic entity if it is anything. This involves the great practical difficulty that we know little of the genetics of protozoan parasites, and, in general, lack even the tools to learn more. A host is not really a good culture medium, if for no other reason than that it almost always possesses enough natural resistance to make it difficult or impossible to establish an infection with a single parasite, and thus establish a clone of the parasites. Hosts are also, of course, infinitely variable themselves since, with very rare exceptions, no two have the same genetic constitution. Not many species of protozoan parasites can yet be easily grown in culture tubes

* Such geographically distinct strains are known, but the isolation must involve the host rather than the parasite.

—still fewer on synthetic media of precisely known composition. Thus, both the experimental induction of mutations and the study of naturally occurring ones are very difficult.

We are still in just about the position in which we found ourselves sixteen years ago, when Taliaferro and Huff (1940) remarked, on the occasion of a symposium not unlike this one: "A review of the genetics of parasitic protozoa is of value chiefly to emphasize the small amount of analytical work that has been done and the great importance of the field for further investigation." I do not see how a real understanding of the problem of intraspecific variation can be achieved except by carefully controlled and executed studies of parasite genetics.

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REGINALD D. MANWELL is Professor of Zoology at Syracuse University, Syracuse, N. Y.

Intraspecific Variation in Parasitic Flatworms

HORACE W. STUNKARD

AT THE outset of our discussion it would be useful, I believe, to stake out the areas and list the items on which there is general agreement. It is admitted that species exist, and that the species is the basic unit in taxonomy. Further, it is agreed that taxonomy has two primary functions or obligations, one of which is to designate each species in a distinctive and permanent manner, so that it is and will continue to be identified by the same cognitive symbol or name. The second task is the formulation of a system of classification which will express evolutionary sequence and genetic relationship of fossil and living organisms. It has been stated that John Ray (1686) first introduced into natural history an exact concept of species, and it pertained to plants rather than animals. At that time and for the next century, the idea of "fixity of species" was accepted; that idea precluded the taxonomic problems which confront us today, and Linnaeus in the *Systema Naturae* was able to name and classify many common animals, which remain as accepted, valid species.

Theories of Evolution

The idea of evolution, foreshadowed in writings of the ancient Greek philosophers, and traced by Osborn (1894) in *From the Greeks to Darwin,* was based on observations that species are not fixed, but plastic entities, composed of individuals that differ from one another and from their parental and more ancestral generations. From his position as superintendent of the Jardin du Roi (1739-1788), Buffon noted the variation in plants and animals, and in his popular *Histoire Naturelle,* begun in 1749, he suggested that the different forms of life have gradually changed under the influence of climate, food, and domestication. His ideas implied a balance in nature, but his contribution was philosophical rather than scientific, since his observations were general and not supported by precise, factual data. The tentative and somewhat vague notions of Buffon were followed by Goethe's (1790), "Versuch, die Metamorphose der Pflanzen zu erklären," in which he confirmed the earlier belief that parts of flowers are modified leaves. This work, together with his subsequent observations on the metamorphosis of parts in plants and animals, led to the conviction that existing organisms have evolved from simpler parental types. The philosophical and poetic considerations of Buffon and Goethe were consolidated into a more precise and better-organized treatise, *Zoönomia,* by Erasmus Darwin (1794). In this work he outlined ten principles which operate in the life-histories of animals, discussed the reactions of organisms to external conditions, the effects of use and disuse, and predicated the error in the idea of fixity of species. Many of his ideas were clarified and amplified by Charles Darwin, who incorporated them into his *Origin of Species* (1859).

But the theory of evolution as we know it, a branching tree with gaps between the branches, was formulated by Lamarck and published (1809) in his *Philosophie Zoologique.* Earlier, as custodian of plants at the Jardin du Roi, he had accepted the idea of "fixity" of species and in his *Flore Française* had devised a dichotomous system of characters for the identification of plants. With the reorganization of the garden (1793), Lamarck was assigned to a chair of zoology and began the study of the animals for which he introduced the term, Invertebrata. Already an experienced, accurate and astute observer, his

investigations were concerned with both fossil and living invertebrates. The persistently recurring and progressive variations, with gradual transformations in successive geological strata, were incompatible with the concept of "fixity of species," and in his *Système des Animaux sans Vertebrès,* Lamarck (1801) first expressed his conviction that living organisms are modified by environmental changes. The idea of evolution was developed and clearly stated in his *Philosophie Zoologique.* His attempt to account for the organization of invertebrates and modifications of their organs as the end-products of responses to stimuli, met with vigorous opposition from orthodox groups, led by Cuvier, who employed slander and ridicule when unable to find satisfactory arguments against his ideas. His use of the word *besoin* was interpreted in an erroneous and perfidious manner to mean desire or longing, and the idea that an animal could change its form merely by wishing to do so was obviously fatuous; but Lamarck had insisted that altered environmental conditions initiated altered requirements on the part of organisms and resulted in altered habits, which eventually led to adaptive changes in form.

The concept of evolution of plants and animals received strong support from the evidence marshalled by Charles Darwin and vigorously presented by Thomas H. Huxley. The fact of evolution is now accepted, but the factors responsible for evolution, and the manner in which they operate, are still controversial. Lamarck recognized several ways in which the environment brings about changes in plants and animals. His attention was drawn to the adaptive character of the responses, which are often direct and immediate in plants, whereas in animals the changes are indirect and result from new uses of pre-existing organs, from the effects of use or disuse, or from physiological adjustments of a more general nature. These changes, occurring repeatedly over thousands or perhaps millions of generations, become established as stable characters. Thus, characters acquired as the results of functional activities on the part of organisms become a part of the hereditary endowment of the species. Darwin noted that mutilations are not inherited; he realized that perpetuation of new species required the inheritance of newly acquired characters, and showed how natural selection operates to direct the course of evolution. He assumed variability as axiomatic and made no attempt to determine the origin of variations. To account for the fact that the gametes transmit all specific features, he supposed that hypothetical units, pangenes, are produced by the tissues and accumulate in the reproductive cells.

Theories of Heredity

Attempts to explain the transmission of hereditary features have been made by many naturalists. After unsuccessful efforts to demonstrate the existence of pangenes, Galton (1875) proposed the theory of "stirp," to designate the total of organic units present in the fertilized egg, some of which pass to the body cells and determine their development, while others remain in the sexual cells. According to this hypothesis, the sexual cells, which transmit the stirp, are not influenced by the conditions of life of the individual. The idea of a particulate, hereditary substance present in gametes was advanced by Nägeli (1884) in his *Mechanisch-physiologische Theorie der Abstammungslehre.* He had sought a material substructure for inherited characters, and Weismann (1892), combining the ideas of Galton and Nägeli, developed the concept of *Keimplasma.* The proposal of Weismann was speculative, lacking in real evidence; the few experiments performed were mutilative and not at all convincing. With the discovery of the chromosomes and their behavior, Weismann localized the *Keimplasm* in the chromosomes and proceeded to analyze the material into its constituent parts, to visualize the architecture of the germ-plasm. According to him, the chromosomes were composed of ids, ids composed of idants, idants composed of determinants, and these in turn

of biophores, the smallest living components. These particles, Weismann declared, "must exist, for the phenomena of life must be bound to an entity of matter." The theoretical concepts of Weismann were critically analyzed by Romanes in his (1899) *Examination of Weismannism,* and Oscar Hertwig (1916) in *Das Werden der Organismen* denounced all theories of biophores, plastidules, and such elementary particles to which special powers or attributes had been ascribed.

The discovery in 1900 of Mendel's earlier publication placed the laws of inheritance on a firm basis, but speculation concerning the nature of the genetic factors continued to be rife. At this time, the observations of DeVries on *Oenothera lamarckiana* led to his theory of mutation, the occurrence of major alterations in specific characters, whereby a species suddenly gives rise to new forms which survive unchanged until the next mutation. He postulated that all new characters arise as a result of mutations; that minor fluctuating variations are not inherited and have no effect on evolution. Natural selection eliminates the mutants that succumb in the struggle for existence. The experimental results of Mendel established the idea of unit characters, which behave independently and are not changed by hybridization. The factors responsible for the development of these characters were designated "genes," a new name for an old concept, but genes were and are hypothetical, and virtually identical with the biophores of Weismann. A synthesis of Weismannism and Mendelism formed the foundation of the genetics of the last half-century. Mutations were presumed to arise spontaneously, fortuitously, and in all directions. New systematic units originated either by mutation or by amphimictic recombination; selection, natural or artificial, determined survival value. Characters acquired as responses to environmental changes were dismissed as of no significance, since they were not regarded as hereditary. Phylogeny was ignored as a profitless if not hopeless study; systematics and evolutionary biology were largely ignored in adoration of the gene. The idea of species became genetic, not Linnean, and although the International Rules of Zoological Nomenclature were accepted, and a species was based on a type specimen, studies were concerned with chromosomes, genes, and unit characters. Genetic theory evolved into a complex superstructure, in which hypotheses, based on assumptions, supported additional hypotheses.

As a graduate student I had been indoctrinated with accepted theory: genes in chromosomes, and characters of the new individual, including sex, determined at syngamy. Then, serious doubts were raised in my mind when Oscar Riddle in 1916 reported sex reversal in birds and demanded to know what happens to the chromosomes of these birds when the sex is reversed. It became clear that often many genes are involved in the formation of a character and that a gene may influence many characters.

Eventually, the relation between genetics, systematics, and evolution attracted attention. It was admitted that certain mutations are minor, resulting in minute changes; that congenital variations may be indistinguishable from acquired ones. In other words, a mutation is merely a variation that proves to be heritable; and since they are usually recessive and retrogressive, the mutation could be identified only in an inbred, second-generation back-cross. The idea that mutations arise spontaneously and fortuitously was challenged as contrary to all scientific experience; events do not happen without cause, and although the cause is unknown, it cannot be dismissed as non-existent. Finally, the progress of cytology and biochemistry demolished the idea of biophores and other living units in protoplasm, and the "gene," I venture to suspect, is merely a stereoisometric configuration of constituents in the protoplasm, which determines the kind and rate of reactions that take place in it. These reactions, predetermined by the substrate and mediated by enzymes, determine the

end-products of successive reactions and direct the course of morphogenesis.

Species Concepts

The reaction against the splendid but unfulfilled promises of genetics led to the integration of genetics with other disciplines in the field of biology. Contributions including *The New Systematics* (1940) *Systematics and the Origin of Species* (1942), *Genetics, Paleontology and Evolution* (1949), *Genetics and the Origin of Species* (1951), and *Methods and Principles of Systematic Zoology* (1953) present a changing concept of the species from a static to a dynamic entity. Although there is almost universal agreement on the actuality of species, a satisfactory definition of the species has not yet been formulated. According to Mayr, Linsley and Usinger (1953), the old systematics was organized around the central position of the species, typologically conceived, morphologically defined, essentially non-dimensional; whereas in the new systematics the morphological definition is replaced by a biological one, which takes cognizance of ecological, geographical, genetic, and other factors, and populations have become the basal taxonomic units. The species is portrayed as consisting of variable populations, capable of interbreeding. Accordingly, species are defined as groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups. Mayr, writing on "Speciation and Systematics" in *Genetics, Paleontology and Evolution,* stated (p. 284): "Species are recognized not on the basis of the degree of difference, but rather on the completeness of separation." Since the idea of interbreeding populations is an integral and essential part of the definition, Mayr continued (p. 284): "It is rather hopeless to arrive at a satisfactory species definition if one wants to include in a single species concept, apomicts, hybrid flocks, obligatory hermaphrodites and asexual organisms. A fairly stable definition may be arrived at for bisexual animals." Dobzhansky, in *Genetics and the Origin of Species* (1951) had stated (p. 263): "Species are tangible natural phenomena. Interbreeding, gene exchange, and the presence or absence of reproductive isolation between Mendelian populations can, however, be studied directly with the aid of the methods of genetics and ecology. Systematists are rarely able to use any of these methods in describing species, and this situation is not likely to undergo substantial change in a predictable future." He pointed out that in groups of sexual and cross-fertilizing organisms, species based on reproductive isolation correspond closely to those recognized by systematists. However, he added (p. 273): "It is not surprising that the groups or organisms recognized as being uncommonly 'difficult' from the standpoint of delimiting species have proved to be mainly those in which asexual reproduction, apogamy, or self-fertilization are the only, or the chief, modes of propagation."

It is clear that a definition which is applicable to only a segment of the Animal Kingdom, to existing, dioecious, interbreeding groups like birds and most insects, is woefully inadequate as a concept of specificity. Moreover, the definitions of the characters employed in delimiting genetic species are often ambiguous and equivocal, e.g., Mayr, Linsley and Usinger in *Methods and Principles of Systematic Zoology* (1953, p. 105) stated: "A taxonomic character may be defined as any attribute of an organism or of a group of organisms by which it differs from an organism belonging to a different taxonomic category or resembles an organism belonging to the same category." But there is no statement as to how to distinguish between categories or to tell whether a certain organism belongs to one or to a different taxonomic category. Moreover, the definition of a taxonomic character is concerned with organisms, whereas the species concept is based on populations. For sheer incomprehensibility and obfuscation note the statement by Curt Stern in the article, "Gene and Character" in *Genetics, Paleontology and Evolution* (p.

13): "A character may be defined as any observable product of genic action." But how one is to tell whether any feature is or is not the result of genic action was not disclosed.

But the idea of genetic species is not new. Lotsy (1916) proposed the substitution of a genetic for the Linnean concept of species which, he declared, is only the product of the imagination, and consequently these groups should no longer be called species but "linnaeonts." Similarly, races or varieties were designated "jordanonts," after the French botanist, Jordan. Commenting on Lotsy's proposal and on his admission that, ". . . in regard to organisms with sexless reproduction, we can never know whether they are species, for that can be discovered only through the analysis of hybridizing experiments," Nordenskiöld (1928, p. 614) observed: "This conclusion of Lotsy's clearly proves that an insistence upon the genetical idea of species can only lead to sheer paradox; he admits himself that only linnaeonts and jordanonts can possess any practical systematic significance. The whole of his reasoning is really a striking proof of the power of language over thought; he wants what is called species to be a genetical entity, and so he comes to a point where he does not know whether species in his sense of the word exist at all in nature." Lotsy's proposal is a barefaced attempt to alter the meaning of words, to give different and sometimes opposite connotations to common terms—a technique long prevalent in the political field, but quite out of place in science.

Charles Darwin in *The Origin of Species* (p. 30) wrote: "Nor shall I here discuss the various definitions which have been given to the term species. No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species." Although he was concerned with only vertebrate animals, one of the most useful and rational statements is that of Simpson (1943) in his distinction between genetic, morphologic, and taxonomic species. Genetic and morphologic species are objective and correspond closely, morphology being an expression of genetic constitution. The taxonomic species, on the other hand, is subjective; it approximates the morphologic species and actually "is an inference as to the most probable limits of the morphological species from which a given series of specimens has been drawn." These individuals are representatives of the morphologic species, and since a working taxonomist is acquainted with only an infinitesimal fraction of the individuals in a species, the limits of taxonomic species remain indefinite and are estimated on statistical grounds. Identification of genetic species is impossible for the paleontologist and impractical, if not impossible, for the student of parasitic flatworms; so for these workers the taxonomic species is derived entirely from morphological data.

Another type of species, and one that deserves further consideration, is the "biochemical species," identified and characterized by serological reactions. Bordet (1899) discovered that the precipitin reaction of Kraus is not strictly specific, since an antiserum may react, not only with the protein used to induce its formation, but with other closely related proteins. Uhlenhuth (1901) extended and quantified the observation; he showed that an antiserum will react more strongly with the antigenic substance used in its formation than with other, related substances, and that the strength of the reaction indicates the degree of relationship between the antigenic substances. Nuttall (1904) made extensive application of the precipitin reaction to problems of animal relationship and phylogeny, noting that the degree of reaction between any particular antiserum and different antigens was correlated with the degree of relationship between the species of animals providing the antigens. Improvements in technique and applications of the method have been made, especially by Boyden (1943) and his colleagues. Wilhelmi (1940) investigated serological reactions and species specificity in certain trematodes and cestodes. He found that species could be

identified with accuracy and that adult and corresponding larval stages of *Parorchis acanthus, Cryptocotyle lingua,* and *Zygocotyle lunata* were practically identical serologically. He predicated (p. 84) that, " 'Species' of helminths may be defined tentatively as a group of organisms the lipid-free antigen of which, when diluted to 1:4000 or more, yields a positive precipitin test within one hour with a rabbit antiserum produced by injecting 40 mg. of dry-weight, lipid-free antigenic material and withdrawn ten to twelve days after the last of four intravenous injections administered every third day." Later, he found that more potent antisera could be obtained by the use of more antigenic material and by extending the length of time during which the injections were made.

The Species in Parasitic Flatworms

The "genetic species" of the new systematics has nothing of practical value for the student of parasitic flatworms. These worms ordinarily do not occur in interbreeding populations; they are hermaphroditic and self-fertilizing; most of them have alternation of hosts, and often two, three, or even four hosts in the life-cycle, in which the sexual generation may be followed by a series of asexually produced generations in very different hosts. For more than forty years I have been occupied with the study of these worms and I have yet to find any formula to replace the one given by Looss (1902) to define species, genera, and higher taxonomic units. The situation is one of the most exasperating and challenging in systematic zoology. The worms cannot be maintained apart from their hosts, and the influence of the host on the parasite can never be completely assessed. At one time it was believed that each species of parasitic flatworm is limited to a single host-species or at most to a few closely related species, but the development of the same species in hosts as distant as reptiles, birds, and mammals has disposed of that idea. Indeed, in most instances we do not know the extent of possible hosts. When an investigator is confronted with similar worms from different hosts, he has no precise way of determining whether he is dealing with one or more than one species. In such variable worms, which have no skeletal structure, and in which the shape is modified by the contraction of different sets of muscles; which may become sexually mature at one-fourth the maximum size and continue to grow as long as they live; in which the morphology is dependent on the degree of maturity; and in which the location and shape of organs are influenced by extension and contraction of the body, by accumulation of genital products (spermatozoa in the seminal vesicle or eggs in the uterus), or even by accumulation of fluid in the excretory vesicle; specific determination of a particular individual may pose an almost insoluble problem.

In the Turbellaria there are relatively few parasites, and practically all of them occur in mollusks, crustaceans, or echinoderms. In the absence of precise information concerning life-histories and possible hosts, problems of speciation are indeterminate. The specific and taxonomic difficulties are illustrated by the study of Stunkard and Corliss (1951) on members of the family Umagillidae. Except for the Turbellaria, all other flatworms are obligate parasites; the monogenetic trematodes are monoxenous, whereas the digenetic trematodes and cestodes have alternation of generations and hosts. The situation in the Monogenea may be illustrated by study of two common species. *Gyrodactylus elegans* is a common parasite on the gills and fins of freshwater fishes; members of a dozen different genera of fishes are susceptible. *Benedenia melleni* (*Epibdella melleni*) occurs on marine fishes; its life-cycle was studied by Jahn and Kuhn (1932), who reported it from a number of possible host-species. Nigrelli and Breder (1934) extended the host-range to include fifty-seven possible species and described the development of immunity to reinfection. With rare exceptions the digenetic trematodes begin the life-cycle when their larvae invade

mollusks; the cestodes when their larvae invade arthropods. It is probable that these life-cycles have phylogenetic significance.

Host-Parasite Interactions

The type of host may affect the parasite in innumerable ways. An excellent discussion of this subject was given by Chandler (1923) in his essay on "Speciation and Host Relationships of Parasites." Members of a single species of parasitic flatworms may develop in a number of different species of final hosts; witness the well-studied trematode parasites of domestic animals that have been taken by emigrants to various parts of the world. As examples I have selected *Fasciola hepatica* and *Dicrocoelium dendriticum,* liver flukes which become mature in a number of possible hosts, and the same facility is probably widespread among other less well-known species. *Fasciola hepatica,* the first trematode to be described and the first for which the life-history was discovered, matures in man, monkeys, sheep, goats, cattle, buffaloes, deer, camels, llamas, elephants, horses, asses, dogs, rabbits, hares, guinea pigs, squirrels, beavers, and kangaroos. The size and morphology of these parasites are profoundly affected by the host-species in which the worm develops. Specimens from a cow, a rabbit, and a guinea pig manifest differences far greater than those usually employed to distinguish between species. The other species, *Dicrocoelium dendriticum,* has been reported from man, sheep, cattle, goats, deer, camels, horses, rabbits, hares, dogs, pigs, and the coypu. Worms from different host-species may be very dissimilar.

A comparable situation obtains among cestode parasites, and again if we consider two well-known species, *Dipylidium caninum* and *Hymenolepis diminuta,* we find that the first develops to maturity in man and in practically all species of the Canidae and Felidae. Millzner (1926) devised a key to seventeen previously described species of *Dipylidium* and five new species which she described from cats and dogs in California. López-Neyra (1929) published a revision of the genus *Dipylidium* in which he attempted to distinguish between the several species. Venard (1938) made an experimental study of *D. caninum;* eggs from a single strobila were fed to larvae of the dog-flea, and the fleas when adult were fed to uninfected cats and dogs of various ages, sizes, and nutritional states. The adult worms were recovered from these experimental hosts and after an analysis of over 10,000 specimens, Venard reported on the variation in twenty-two characters which had been utilized as specific features. On the basis of normal variation as observed in *D. caninum,* he recognized only three valid species: *D. caninum* (Linn.); *D. buencaminoi* Tubangui, 1925, which differs from *D. caninum* only in size of eggs, a difference that may represent an error in measurement or transcription; and *D. otocyonis* Joyeux, Baer and Martin, 1926, which was distinguished only on the size and distribution of the rostellar hooks. Members of the genus *Hymenolepis* infect man, dogs, and most wild and domestic rodents. The number of described species is enormous, some 380, and I feel confident that an experimental analysis of variation in *H. diminuta* and *H. nana,* similar to the one done by Venard on *D. caninum,* would relegate many of the described species to synonymy.

In addition to specific differences, the physiological condition of the host may profoundly affect the flatworms harbored by it. A well-nourished animal may expel a parasite which could remain and mature in an undernourished and emaciated host. I raised *Cryptocotyle lingua,* normally a bird parasite, to sexual maturity in a gaunt and meager female rat which had just weaned a large litter, although the young rats and other well-nourished individuals were completely refractory. Anne Hager (1941) studied the effects of dietary modifications of host-rats on the tapeworm, *Hymenolepis diminuta.* She found that vitamins of the G-complex were necessary for normal egg-production and that crowding reduces the size and repro-

ductive ability of the parasite. This work was continued by Chandler (1943*a*, *b*) and Addis and Chandler (1944), who measured the effects of different diets and dietary deficiencies on the growth and fecundity of *H. diminuta*. They found that diets deficient in G-vitamins caused stunting of the worms in female, but not in male rats, and Addis (1946) reported that worms in castrated male or female rats on vitamin-G-deficient diets developed normally if the host was supplied with testosterone. Beck (1952) reported on the effects of gonadectomy and gonadal hormones on singly established *H. diminuta* in rats.

The presence of a previous or concurrent infection may seriously affect the parasite. Miller's classic studies (1931-1935) provide a conspicuous example. If an enormous number of cestode eggs, *Taenia taeniaeformis,* is given at one time to a rat, the larvae localize in the liver and develop, with the result that the rat looks like a football and about one-half the total weight is liver and parasites. On the other hand, if a single cysticercus is established in the liver of a rat, no others will develop. Artificial immunity can be produced by serum from infected animals, and young of infected mothers manifest a considerable degree of resistance to infection with the onchospheres. Previous infection with strobilate stages of the cestode provide little or no protection in cats against reinfection or superinfection by sexual stages of the worm. Willey and Stunkard (1942) reported on pathology and resistance, in terns and dogs, to infection with the heterophyid trematode, *Cryptocotyle lingua.* The worms denude the epithelium of the villi, producing exudation of mucus, pressure atrophy, necrosis, and hyperplasia of fixed tissue elements. After a period of acute catarrhal enteritis, if the animal survives the initial infection, resistance develops, "self-cure" is effected, most of the worms are voided, and regeneration of the mucosa repairs the damaged parts. Injury to the mucosa is greater, and immunity develops more slowly, in dogs than in terns.

Difficulties Presented by a Diversity of Life-Stages

In discussing digenetic trematodes, I mentioned that the adult worms may develop in diverse host-species and are affected accordingly, both physiologically and morphologically. But these trematodes have one, two, or even three intermediate hosts, in the first of which there is a series of asexual generations. Referring to the same two well-known species, asexual generations of *F. hepatica* have been reported from species of *Lymnaea, Galba, Succinea, Pseudosuccinea, Fossaria, Praticolella, Bulimus, Isidora,* and *Ampullaria.* According to Mapes (1951), in different parts of the world, *D. dendriticum* uses fourteen different species of terrestrial snails belonging to five different families: Helicidae, Enidae, Chondrinidae, Vitrinidae, and Ariophantidae. Since that time, Krull and Mapes (1952) have worked out the life-cycle of the parasite in New York state, where it has recently become established, and found that the first intermediate host there is *Cionella lubrica,* member of a sixth family, Cionellidae. In any particular area one molluscan species is preferred as first intermediate host, although in another area a different one may be selected. Examples are provided by species of *Schistosoma.* It is agreed that *S. mansoni* was introduced into the western hemisphere with the slave trade. In Africa the parasite uses species of *Planorbis, Physopsis,* and *Isidora* as first intermediate hosts. In the West Indies and South America, *Australorbis glabratus* and *Tropicorbis centimetralis* are the first intermediate hosts. Certain strains of *A. glabratus* apparently are not easily infected, whereas the one I maintained in the laboratory for three years (Stunkard, 1946) was uniformly susceptible; every snail exposed, whether juvenile or adult, was readily infected. In Egypt, the natural host of *S. mansoni* is *Planorbis boissyi,* but I was unable to infect this snail with the Puerto Rican strain of *S. mansoni;* similarly, miracidia of the Egyptian strain of *S. mansoni* would not infect my representa-

tives of *A. glabratus*. The natural hosts of *S. japonicum* in the Far East are species of *Oncomelania* and *Katayama*. In the paper just cited, I reported the infection of *Pomatiopsis lapidaria* with miracidia of *S. japonicum*, an observation which was confirmed by Berry and Rue (1948) at the National Institutes of Health.

Turning to the intermediate hosts of cestodes, the first intermediate host is typically an arthropod and the simpler or more primitive tapeworms regularly have a second intermediate host in the life-cycle. Only the cyclophyllidean species have dropped the second intermediate host, and certain species of *Hymenolepis* may dispense with both intermediate hosts, but the deletion of the second intermediate host is clearly an adaptation to terrestrial life. In the two species cited earlier, *D. caninum* uses various species of fleas and lice as intermediate hosts while *Hymenolepis diminuta* is far more versatile. The reported intermediate hosts include: the lepidopteran species, *Asopia farinalis, Tinea granella, Tinea pellionella, Aglossa dimidiata*, and *Aphornia gularis;* the earwig, *Anisolabis annulipes;* the diplopods, *Fontaria virginiensis* and *Julus* sp.; the fleas, *Ceratophyllus fasciatus, Xenopsylla cheopis, Leptosylla segnis, Ctenocephalides canis,* and *Pulex irritans;* the cockroaches, *Periplaneta orientalis, Periplaneta americana,* and *Blatella germanica;* and the coleopterans, *Tribolium castaneum, Ulosonia parvicornis, Aphodius distinctus, Anobium paniceum, Akis spinosa, Scaurus striatus, Tenebrio molitor, Dermestes peruvianus,* and *Geotrupes sylvaticus*. It is abundantly clear that flatworm parasites are able to acquire new hosts, and that they change hosts with differing ecological situations. It is equally clear that development in different host-species and under different physiological conditions of the individual host may profoundly alter the parasite. In many instances, varieties or races peculiar to certain hosts, hostal varieties, may be recognized, but there is no sound reason to believe that they represent different species.

The versaltility of any given genetic constitution is amazing. The genotype can give rise to all the types of cells which make up the organism; and arrange the differentiated cells into many diverse organs and organ systems. A single genetic constitution can produce both a polyp and a medusa; a caterpillar and a butterfly; or a tadpole and a frog. Similarly, a given genotype can give rise to a miracidium, a sporocyst, a redia, a cercaria, and a sexually mature trematode; while another may yield an onchosphere, a coracidium, a procercoid, a plerocercoid, and then a mature strobila, or the procercoid and plerocercoid stages may be replaced by a cysticercoid or a cysticercous in those tapeworms which have no aquatic stage in the life-cycle. Typically the cysticercoids occur in invertebrates, while the bladderworms develop in vertebrate intermediate hosts. Because of the extensive convergence and divergence in trematodes and cestodes, morphological similarity does not have the significance that it does in free-living species. Distantly related forms have often been associated and closely related ones separated into different families. The identification of sexually mature specimens of parasitic flatworms poses hard and perplexing problems, but the identification of larvae is even more difficult, and the correlation of larval and adult stages has been accomplished only in recent years and in relatively few species. Larval structures may be temporary, evanescent adaptations, the systematic importance of which is often questionable. Witness the types of tails in the larvae of digenetic trematodes, used by Lühe (1909) as a basis for the classification of cercariae, and the diversity in different members of the same family, discovered by the brilliant experimental researches of Cable (1953, 1954) in the Fellodistomatidae, of Goodchild (1943) in the Gorgoderidae, of Patten (1952) in the Dicrocoelidae, and of Robinson (1949) in the Brachylaemidae. Larvae have fewer and less distinct taxonomic characters than adults. Indeed, Sewell (1922) declared that no description of a cercaria

prior to the work of Cort (1914) was sufficiently complete and definite to permit the certain recognition of the species. Moreover, adult and larval stages of the same species have often been described under different names, and no taxonomic work should be accepted as conclusive until all stages in the life-cycle of the species are known.

Members of a single species may differ so much, as a result of development in different host-species, invertebrate and vertebrate, or of different physiological conditions in host-individuals, that the extent of variation is known for few if any species, and the study of Beaver (1937) on *Echinostoma revolutum* may well serve as a model for further work. In a similar and more extensive study, Rankin (1938) examined over 1,500 salamanders of some twenty different species for brachycoelid trematodes. This material was supplemented by specimens from various sources. Observations were made on both living and preserved specimens, and worms from twenty-six host-species in fifteen genera were compared with reference to twenty characters. As a result of the study, Rankin could find no gaps to separate species; the variations were continuous, and so eighteen named species were regarded as identical with *Brachycoelium salamandrae* (Froelich, 1789) Dujardin, 1845, one of the oldest known species and a common parasite of frogs and toads in Europe. Rankin was obviously following the dictum of the late Maurice C. Hall, "If you can't key it out, it is the same thing."

The study of preserved material introduces a further complication into the study of variation. Different methods of fixation can produce amazing effects upon the morphology of parasitic flatworms. Contortions undergone by specimens in killing fluids can result in bizarre individuals which show little resemblance to their normal structure. To avoid such contractions, worms are often fixed under the pressure of a coverglass or slide but such specimens, while they are useful for study of general morphology, are distorted, and measurements of such flattened specimens can be very misleading. Measurements of a pressed specimen can sometimes be 100 per cent greater than those made on the same specimen in a contracted condition. Illustrating this point and discussing the taxonomic problem of pseudophyllidean cestodes of marine mammals, Stunkard (1948) wrote (p. 211):

> Some thirty-three species of pseudophyllidean cestodes have been described from seals and sea-lions but the descriptions are so incomplete and imperfect that it is virtually impossible to recognize any of them with certainty. Redescriptions of species, on the basis of incorrectly determined specimens, have undoubtedly added to the confusion. In the absence of information concerning life-cycles, consideration must be given to the possibility that representatives of a single species may complete their development in different host-species and furthermore that, as a result of development in different hosts, individuals of the same species may manifest differences in size and shape, in rate of growth and sexual maturity, and in extent of development of various tissues and organs. Consequently, specific determination of specimens presents a particularly difficult problem. The pseudophyllidean cestodes of seals and sea-lions have been assigned to nine different genera, but the generic concepts are so indefinite and their limits are so poorly defined that there is no agreement concerning either the number of valid species or the generic groups to which they should be allocated.

It was realized a century ago that sexually mature specimens comprise only a portion of the life-cycle of parasitic flatworms, and it is now clear that specific descriptions must take cognizance of the asexual generations and larval stages. Uncertainty in specific determination, and inability to distinguish between species of adult worms, both trematodes and cestodes, led me to undertake life-history studies, in order to obtain more complete information on which a judgment could be made. Inability to determine the limits of taxonomic species from morphological data caused me to turn to the study of biochemical species and encourage Wilhelmi in his studies of the precipitin reaction in trematodes and cestodes.

Summary

From the data presented, it must be apparent that at present we have no ade-

quate or satisfactory means of measuring intraspecific variation in parasitic flatworms. The precise limits of specificity will remain uncertain until the factors which influence the developmental and morphological features of these parasites are known and evaluated. Since the worms are hermaphroditic and self-fertilizing, and asexual generations alternate with sexual ones, the idea of recognizing and defining genetic species is fatuous and illusory. I know of no more futile effort than fishing for specific characters in a cestode or trematode gene-pool. When life-cycles have been worked out, when larval stages and asexual generations are known, when the ranges of possible intermediate and definitive hosts are determined, and the effects on the parasite of nutritional and other physiological conditions of the hosts have been assessed, we can begin to define morphological species with real assurance. In the meantime, specific determination remains exceedingly difficult. Host varieties may be recognized, but in my opinion, subspecies of trematodes and cestodes have no meaning. The problems of intraspecific variation in parasitic flatworms are formidable, but not insuperable.

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HORACE W. STUNKARD is a Research Associate at the American Museum of Natural History, New York, and Professor Emeritus of Biology, New York University.

Intraspecific Variation in Parasitic Nematodes

M. B. CHITWOOD

THE problems of intraspecific variation in parasitic nematodes are similar to those of the study of other internal parasitic animals, and yet they are in some ways unique. The systematic nematologist rarely has the opportunity to make extensive studies on fresh, unfixed specimens because parasitic nematodes cannot be kept alive and in good condition for any great length of time. Thus, more often than not, he must make use of the available resources, which consist of a motley assortment of haphazardly fixed, often decomposed, sometimes mutilated specimens and an equally motley assortment of published descriptions. It is a well-known fact that greater changes can take place in fixation than actually occur between species or even genera. Since the description of new species is a rapid road to fame, the result has been a confusion of new species, many of which are based on nothing more than misinterpretations, intraspecific variation and artificial concepts, or on failure by the author to search the literature. Indeed, the literature is not always readily accessible. Since in the field of nematology there is no pattern by which to determine the constitution and limitation of speciation, an unrelated assortment of characters are used, there being not even a gentlemen's agreement as to which characters have value for species delineation. Consequently we are frequently frustrated by descriptions in which an overall picture of the nematode is carefully avoided, and many important characters are not even mentioned. Poor sketches, and I use the word advisedly, or poor photographs add to the confusion.

We are all familiar with the arguments at to what constitutes a species. Patterson and Stone's definition (1952), which states "A species consists of the members of a population or group of populations which can exchange genes freely with each other, but which can cross to no other form or population sufficiently to lose its genetic identity," covers the modern concept, but for practical purposes a species must be a morphologically recognizable entity.

We have all read the statement, made with the utmost disdain, that classification is artificial. This I grant—it is an arbitrary structure to some extent, but much of that structure is based on careful and intense studies which substantiate it. Let us, please, not lose sight of the fact that it is a structure built for the very practical purpose of providing us with an understanding of the relationships of organisms and with a convenient, if not always sound, parking place for them. Let us not erect such complicated structures that they defeat the very purpose for which they are intended, or we must have a nomenclature for taxonomists, another for physiologists, and still another for geneticists.

Nematology is still struggling along with the monotypic concept of speciation, and I like it that way. Not nearly enough monographic work has been done to show a crying need for the polytypic concept, if it exists. I, personally, am opposed to the use of the latinized trinomial and much prefer the varietal designation, based upon host wherever possible, and without species and subspecies validity. Subgenera are too frequently merely an interim step to the designation of genera, and subspecies merely add to the confusion.

Let us consider the case of *Ascaris lumbricoides*. For years, efforts have been made both experimentally and morphologically to distinguish between the human strain and the swine strain. Recently Sprent (1952) has made an attempt to divide them on the basis of the fact that

the pig ascarid has bigger and better teeth. Maybe it depends upon how many other parasites the pig has, how much food is available, and how hard the ascarid has to work for a living. Maybe the ascarid of man has to work harder to get back to the gut and so wears out his teeth faster, or, perhaps, as men now eat less like pigs, their parasites may be becoming less like those of the pig. Before we decide that there are two separate and distinct species involved, I should like to see artificial insemination tried. Although ascarids are difficult to study because of their size and thick skin, most nematodes *can* be studied microscopically.

B. G. Chitwood (1938), in separating the genera *Mastophorus* and *Protospirura*, brought out the problem of intraspecific variation in these genera. Intermediate hosts, insects, are required for this group. Baylis attempted to use stomatal length in *Mastophorus* as a specific character, and this seems reasonable until one encounters a specimen with the lips completely everted or completely withdrawn. Then you have a new species. This is artificial variation, but we cannot ignore it. Spicule length has been used as a character, but the variation in one lot of material can be too great for this to be of any significance. The number and character of genital papillae are also variable. The only reasonably constant character on the basis of which these so-called species can be distinguished is the sharpness of the teeth. Chitwood considered differences in this character significant only at a varietal level. The use of physiological and genetic factors is very interesting and may be valuable for substantiating relationships. This remains to be seen.

Factors Influencing Variation

A careful study of all specimens or of standard aliquots, or of enough random samples from each collection, should allow the plotting of normal deviations as well as reveal the presence of anomalies or even of hybrids. We must broaden our concept of species by studying more specimens for the variations and the factors that may influence them. Some of these factors are well known; others have scarcely been explored.

Sheer ignorance confounds us at every turn. A few responsible parasitologists have made valuable contributions through their studies extending the host ranges, measurements, number of papillae, and other characters. Some have carried their extensions to the point of absurdity.

The influence of geographical and ecological factors has certainly not been adequately explored for an understanding of the development of species and their relationships. This study has been complicated by the fact that since the earliest migrations of man, he has taken his domestic animals, his pets, and his pests with him, until now they are spread over the face of the earth, and each has taken his parasites with him. In the past century the worldwide movement of man and animals has increased tremendously, and yet it has only been within this period that the study of parasitic nematodes has been extended over the world. We have no collections of parasites from our native wild ruminants taken before their ranges were contaminated by domestic animals.

This man-made movement is not, however, the only factor. There is evidence that Asiatic and European parasites were here before the white man came. In 1950, Mr. McIntosh and I reported on the finding of the Russian sturgeon nematode *Cystoopsis acipenseri* from a sturgeon collected from Bonneville, Oregon. More recently, I received a species of an oxyurid nematode from a ground squirrel in Utah, belonging to a genus which had previously been recorded only from a small rodent on the eastern banks of the Caspian Sea.

Size, as a species criterion, is useless except as a relative and proportionate concept, since size may depend upon any one of a large number of factors. These are size, age, physical condition, metabolic rate, and food supply of the host at the time of the entrance and growth of the parasite. Most of these factors have been inadequately explored; indeed, it is mostly in the realm of veterinary parasitology that we have any experimental

evidence to support our postulations of intraspecific variation in nematology. Immunological studies tend to prove that a parasite of the second or subsequent invasion will be smaller than those of the first infestation. Obviously, in many instances, the amount of food available is going to play an important role in the definitive size of the adult parasite. *Gongylonema pulchrum* may infest a variety of hosts, and its egg size may vary surprisingly when it lives in different hosts. Since many nematodes are known to pass freely among the Ruminantia, it is probable that the size of the specimens of the first invasion of a new host will be directly related to the parasite's affinity for the new environment. The parasites picked up by wild animals in the late winter or early spring will find a scant food supply if the host is in a state of near starvation, whereas those picked up in summer and fall may find the peak of plenty and, therefore, an optimum condition. The difference in the size of the parasites of these invasions can be phenomenal.

Crowding affects the size of some nematodes tremendously and in others is apparently a negligible factor if it is not lethal. In the mermithids, crowding can result in the absence of females. This is, of course, true of some other nematodes but not so dramatically. In cultures of free-living nematodes one finds a great increase in overall size of the nematodes up to a certain degree of crowding, beyond which size diminishes constantly as the supply of food is exhausted. In the larger nematodes the size of the esophagus remains fairly constant in relation to the normal size, the increase being largely in gut and reproductive organs. This results in completely different body proportions. The females of many parasitic nematodes continue to increase in size after reaching maturity.

Taxonomic Assessment of Variation

The description of a new species based on one or two specimens taken from a large collection and differing in one single characteristic in one sex is ridiculous. Several years ago I received a collection of *Cruzia* from a turtle. Shortly before that time I had been checking *Cruzia testudinis* for characters with which to differentiate it from *Cruzia tentaculata,* so I was quite familiar with the number and arangement of the genital papillae. I mounted a male specimen from this material and was amazed to find the pattern quite different from that of any *Cruzia* I had seen previously. After careful study, measurement, and the making of sketches, I placed the specimen in a small vial and mounted other males. They were all typical *C. testudinis.* The original specimen when remounted was, by chance, reversed. On the one side it was a typical *C. testudinis;* on the other it was a "new species." Had I been working with a permanent mount, and many people do, I should never have known that the specimen was normal on one side. How many such specimen are types of new species? On the other hand, it is not to be denied that there are occasionally accidental infections, and that many hosts normally have more than one species of a genus, as, for example, the numerous horse strongyles and the multitudes of trichostrongyles present in sheep and goats. This is more or less to be expected since the horse has practically covered the earth and the trichostrongyles are apparently quite undiscriminating in their passage from one ruminant to another. Apparently the domestic animals have provided a cumulative reservoir for the parasites of other closely related animals, and the sheep and goats, like sponges, have absorbed most of them.

The protostrongyles, on the other hand, appear to be very host-specific and do, in fact, provide us with our most outstanding example of sympatric species. *Protostrongylus stilesi* lives in the parenchyma of the lungs of sheep, whereas, *P. rushi* lives in the bronchii; and, so far as there is any evidence available, there is no interbreeding nor any encroachment on the territory of the other species. Yet the larvae of these two species must travel the same path to reach their definitive location. The fact that the protostrongyles require an intermediate host may account

for some of the changes which have resulted in the different species.

One of the most interesting cases involving the question of intraspecific variation is that of *Haemonchus contortus,* the common stomach worm. This species was first described by Rudolphi in 1803. Since that time it has been reported from no less than 41 different hosts, covering practically the entire Ruminantia, as well as horses, pigs, bears, and some spermophiles. It is world-wide in distribution. It would, of course, be impossible to check every one of these reports for a correct identification, but it is reasonable to assume that this species will take up residence wherever possible. In 1893, an Australian named Place separated the ovine strain from the bovine strain, naming the latter *Haemonchus placei.* Subsequently this name was synonymized and the matter remained dormant for many years, until Roberts, Turner, and McKevett (1954) again attempted to separate the ovine and bovine forms. They published a rather extensive but inconclusive paper showing differences, mostly in size of structures such as length of spicule and length of tip of spicule to spur; those structures of *H. contortus* were stated to be less than a given measurement, and those of *H. placei* greater. They also found that the vulvar process of the sheep strain tended to have the linguiform process, whereas those of the cattle strain were more often knoblike. They also showed that there is a consistent difference between most of the larvae. An experiment was run in which the progeny of one female of the linguiform type was fed to a worm-free lamb and the progeny of one female of the knob type was fed to a worm-free calf. They also fed sheep-strain *Haemonchus* to cattle and cattle-strain *Haemonchus* to sheep and found that each remained faithful to its type regardless of host. In addition, some cattle strain was mixed with sheep strain and fed to each host. No intermediate forms were recovered, and the worms collected remained visually separable into sheep forms and into cattle forms. They specifically state that in natural infestations, however, all of these differences are not so clear-cut. After spending a great deal of time perusing this paper and in examining specimens from cattle, sheep, goats, deer, reindeer, musk ox, and buffalo, I believe two conclusions can be drawn from this work. First, that, in Australia, there is perhaps an ideal condition for the separation of the sheep and the cattle types of *H. contortus,* which may eventually result in differences at the species level; and second, that the *Haemonchus* in Australia may differ from the *Haemonchus* found in both domestic and wild ruminants in the United States.

The *H. contortus* found in North America agrees with the *H. contortus* from a goat from Venezuela and from a gnu from South Africa. In every host except the musk ox and buffalo (and there is limited material from each) there have been three distinct types of females, specifically, those with a linguiform process, those with a knoblike projection, and those with no vulvar projection. The results of these observations favor the assumption that the females with the linguiform process and those with no vulvar projection are the basic types and that the females with the knoblike projection may be a hybrid. We must also consider the fact that the females of some other trichostrongyles may have vulvar processes of varying shapes and sizes (*Skrjabinagia odocoilei* (Dikmans 1931) for example).

In 1955 Bremner, using squash techniques, was able to demonstrate that the cattle strain of *H. contortus,* in Australia, had two very large chromosomes in the females and one large one in the male. The giant chromosome was not present in any of 67 specimens examined from the goat, but 6 specimens of the sheep strain had them. Could the sheep strain be a cross between the cattle and the goat forms? Could it be that originally there were two similar species, one with a process and one without a linguiform process? And did they find that they could all live together like one big happy family, or is this merely a case of intraspecific variation? Whatever it is, whether it be one species or a species complex, it is

probably never going to separate itself out unless perhaps eventually in Australia or in some place where only one host is available. At any rate, we are faced with the problem of what to call it, or them.

Dictyocaulus viviparus, the common lungworm of cattle, was first described by Bloch (1782) as *Gordius vivipara.* It has since been described from at least 23 other hosts, including most of the native North American and many African ruminants, as well as pigs, horses, sheep, and *Microtus.* Dikmans (1936) placed in synonymy with *D. viviparus, D. hadweni* Chapin, 1925, from *Bison bison, D. ekerti* Skrjabin, 1931, from reindeer in the U.S.S.R., and *D. khawi* Hsü, 1935, from pigs in French Indo-China on the basis that the morphological differences between them are too slight for each to be considered a separate species. The females are indistinguishable, but in the males there is considerable variation in the dorsal ray of the bursa, and some slight differences in the measurement of the spicules. Since the mature males range in length from 17.34 to 43.4 mm. and the females from 23 to 72 mm., this variation makes length a useless character. The above-mentioned artificial variations may result in an almost total absence of the mouth cavity, in a difference in the position of the head papillae, and in the size of the excretory glands. The size of the bursa depends, to some extent, on its state of contraction or expansion. *Dictyocaulus,* unlike other lungworms of ruminants, requires no intermediate host, but experimental evidence of cross-transmission between domestic and wild ruminants is lacking despite the opportunity for contamination of ranges.

The spicules are considered the only valuable character in distinguishing the species of *Setaria;* yet one frequently encounters specimens in which the spicules are so lightly sclerotized that they bend with the slightest manipulation of the specimen, and as a result their study is difficult if not impossible. The lateral and terminal projections on the tails vary in size and character, but little attention has been given to their position. Artificial variation of the head projections renders them useless as a character.

Variations, both real and artificial, exist throughout the Nematoda, and the interpretation of the value of any one character which is useful in one group may have no significance in another.

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MAYBELLE CHITWOOD is a parasitologist engaged in the study of nematode classification in the Parasite Laboratory of the Animal Disease and Parasite Research Division, U.S.D.A., A.R.S., A.R.C., Beltsville, Maryland.

Intraspecific Variation in the Parasitic Acarina

G. W. WHARTON

BECAUSE parasitic animals have many morphological and physiological adaptations that are peculiar to their parasitic mode of life, they are frequently considered to be essentially different from free-living animals. This symposium is one manifestation of a vague but widespread intuitive recognition that parasites are quite different from free-living forms. A search for yet to be enunciated basic principles of parasitology is another symptom of the belief that parasites are not at all like other animals (Huff, 1956). Systematists as well as parasitologists seem to share such views (Mayr, 1949*a*; Carter, 1949). It is axiomatic that each kind of animal is different from each other kind and that animals that can be grouped on the basis of one or another of their properties will be similar to each other in at least certain respects, but it is also true that the general biological phenomena of natural selection, mutation, evolution, adaptation, and adjustment that are responsible for organic diversity will apply to all animals. Intraspecific variation in parasitic animals should therefore be of the same type as that found in free-living animals. There is no more reason to expect fundamental peculiarities in intraspecific variation among parasitic animals than there would be to expect peculiarities among predators, herbivores, or scavengers.

Genetic Organization of Species

Like so many controversial and, therefore, interesting topics for discussion, semantics, or meanings of words, looms large in consideration of intraspecific variation. To the systematist the differentiation of intraspecific as opposed to interspecific variability is essential to his work. The recognition of differences among a group of specimens and the description of these differences do not constitute a difficult task. It may be time-consuming; it is of utmost importance. It must be done with extreme care, but it does not require extensive background, brilliant logic, or original thought. The part of systematic work that does require extensive background, brilliant logic, and original thought is the evaluation of the observed differences. In this evaluation, the most difficult problems arise in determining whether or not a difference is specific or subspecific, generic or subgeneric, familial or subfamilial, etc. Specific versus intraspecific differences are of special interest, because to most systematists the species is the basic taxon. The part that semantics plays in this discussion is the meaning of the word "species" (Mayr, 1949*b*). What is a species? So many systematists have attempted to give definitions, or have in fact given definitions of species, that one more definition hardly seems to be a contribution. As a matter of fact, it seems that there is only one criterion that all systematists will accept as essential in differentiating between specific and intraspecific taxa. This is, that all systematists consider that the species has a genetic basis. If two animals have the same parents, they belong to the same species. It is epecially appropriate that systematists put great emphasis on the gentic organization when they are considering the theoretical aspects of speciation, because it is the genetic organization that is responsible for the most outstanding characteristic of a species, or at least, most outstanding in my mind. Few things in this world extend as long in time as do species. It would, indeed, be difficult to give a real estimate of the length of life of the average species; how-

ever, from the available knowledge it seems that the average life span of a species is of the order of magnitude of a million years (Simpson, 1953). The only attribute of a species that endures for a million years is the genetic organization that is responsible for the hereditary patterns that are passed on from one generation to another. It should be emphasized that it is the pattern, the organization, and not the material that lasts so long in time; and it is the pattern, the organization, that is responsible for the development of the traits that serve as the basis for specific differentiation.

Definitions in science are usually given in pragmatic terms. When the scientist wishes to define something, he can best do this by telling us how to measure it. Individual species are defined on the basis of the properties of specimens of the species that are available to the definer or describer. Most definitions of species are in anatomical terms; but physiological properties, geographical distribution, peculiarities in life cycles, serological reactions, and many others may be used. The species, nevertheless, is not a particular morphological entity. It is not a group of physiological properties; it is not a group of specimens. Though, in recent years, it has become fashionable to consider a species as a potentially interbreeding population, species are more than interbreeding populations or groups of interbreeding populations. To appreciate the real nature of species, it is necessary to go back to the genetic organization. In considering the genetic organization, many systematists have thought of the genes as being entities that added together can be responsible for the species. The genetic organization is frequently spoken of as a pool of genes from which each individual belonging to the species receives his hereditary characteristics (Dobzhansky, 1951), but I would again like to submit that species are not gene pools but are based primarily on the total organization, the pattern or organization being more important than the individual gene.

At the present time, theoretical systematists are primarily concerned with populations, with gene pools, and with the dynamics of changes in the morphological characteristics of representatives of species as they vary from one geographical area to another, from one ecological niche to another, or from one geological stratum to another. This is particularly true of the systematists who are working on groups of animals that are well known, that are represented by relatively few species, and whose properties are well charted. The more conventional systematics, that is the systematics used at the present time by people who are working on groups of animals that are poorly known because of the tremendous numbers that exist, is still paying quite a bit of attention to things that are called "systematic characters." In most parasitic forms, these systematic characters are anatomical features, details of life cycles, and host and geographical records. Unfortunately, a good bit of our classification is also based on so-called systematic characters. In a particular group of animals, a certain characteristic will be said to be of specific value. This is because some systematist has found that a particular feature will consistently be present in specimens of one species and be absent from specimens of another species. These systematic characters are actually like the trademarks on the cans on the shelves of the supermarket. When you go to the supermarket and you look at the cans, they may all be the same size and about the same weight, but the labels on the cans say that this one is peaches and that one is applesauce and another is plums. Systematic categoric characters are of this sort. They are merely trademarks that enable us to recognize and differentiate a specimen as belonging to one species or another. It is unfortunate that much of our clasification of animals is based primarily on these trademarks rather than upon all of the properties of the animal concerned. Trademarks are particularly useful in recognizing specimens as belonging to a given species.

Most of our errors in grouping animals have resulted from imperfect knowledge and the use of so-called taxonomic characters for the purposes of classification with failure to consider all of the known properties. As a matter of fact, in making a classification of animals, it is essential that the properties used are those that give a good picture of the genetic organization of which we have been speaking so much. We assume that the properties of specimens reflect the genetic organization.

Much is now known about the nature of genetic organization, about how these patterns are maintained, how they are transmitted from one generation to another, and how they may be changed or modified. In assessing whether or not a particular group of specimens belongs to the same species, in any group of animals, it is extremely desirable to think about the posibility and the plausibility of these animals' possessing essentially the same genetic organization or at least the same as far as is usually accepted for a specific group. If it is obvious that the specimens do not all have the same fundamental genetic organization, then it follows that they do not all belong to the same species. However, if they do show some regular variation and yet the evidence is that they may belong all to the same species, then the variation should be of the type that is possible as a modification of a specific genetic pattern.

It should be emphasized at this point that the same sort of characteristic may not indicate the same divergence of genetic pattern in all species in even rather closely related species. For example, in the family Trombiculidae, a number of the species are characterized as having a certain number of setae in a row posterior to the dorsal plate. Those species that have six hairs or setae in this row show relatively little variation. Occasionally a specimen with seven setae in this row may be found, but this is extremely unusual. On the other hand, a fairly high proportion of specimens that have an average of eight setae in the first dorsal row will be variable. When the average number of setae in this row is as many as ten, more specimens will have a number different from ten than specimens that have only ten, despite the fact that the average number of setae will be ten. Thus, in species with six in the first row, this number makes a good specific character. It can differentiate those species with six from those species with eight and from those species with more than eight. An average number of eight setae in the first row is also a good specific character; however, species that have ten or twelve setae in the first dorsal row cannot readily be differentiated on this property. This property is too variable among the specimens of such a species to be of importance in the recognition of individual specimens. It is, of course, not unimportant in the recognition of a series of specimens. Nevertheless, these characteristics would be poor specific characters because the actual numbers do not reflect the basic genetic organization. The evaluation of characters is extremely important in working out the systematics of any group of animals. In this evaluation, the breeding mechanisms of the organisms must be taken into account.

Effect of Breeding Pattern

In the parasitic mites, there are three fundamentally different breeding patterns, the first of which is exemplified by the family Trombiculidae and related families. In the family Trombiculidae, the only parasitic stage is the larval stage. Larvae attach themselves to hosts and take a single meal. After they have had their larval meal, they drop from the host and bury themselves in the ground. They then moult into nymphs. The postlarval nymphs and the adults that are developed from them are free-living, predaceous animals that are dependent upon the properties of the soil for their survival. Reproduction in these forms takes place in the soil, and the distribution of these mites is characteristic of the distribution of free-living organisms. These mites will vary from one locality to another. The

variation will be clinal in nature in some cases (Farrell, 1956) and non-clinal in others (Brennan and Wharton, 1950). The intraspecific variation in these forms is therefore quite similar to the intraspecific variations and differences that occur in birds and mammals, some of their normal hosts. It is possible to use the same techniques in dealing with parasitic Acarina of this type as are used with the systematics of other of the free-living organisms, and as a matter of fact, a few polytypic species of trombiculids are recognized although in most cases names for the subspecies have yet to be proposed.

The question of host-specificity in such forms is a difficult one. The spectrum of available hosts or suitable hosts for each species is relatively large. The tastes of the larvae, however, are not universal. Each host is more likely to be parasitized by certain species than it is by other species, and furthermore each species seems to have a rather characteristic distribution on each particular kind of host. For example, our common pest chiggers are found beneath the scales of snakes, in the axillae and groins of turtles, on the legs of birds, on the toes of rabbits, and at points where the clothing is tight on man. Host-specificity in the family Trombiculidae is a matter of the suitability of the host as a source of food and the availability of the host in terms of ecological niches. For example, some species such as *Euschöngastica indica* (Hirst) are commonly found only in trees or rather the soil-like accumulation of material in trees fairly well up from the ground (Wharton and Fuller, 1952). Hosts that do not climb trees are not parasitized by the larvae of this species.

Other parasitic Acarina, instead of breeding in the soil without regard to the distribution of their hosts, breed regularly in the nest of the host. As an example of the mites of this sort, we shall take the family Dermanyssidae. The typical life cycle of a dermanyssid involves a number of feeding stages and a number of stages off the host. They live more or less like bedbugs, in the nest of the host, and come to the host only to feed. Reproduction in these forms occurs while the parasites are off the host; thus in any one nest, a considerable amount of inbreeding will result, and the individuals that are collected are similar to the individuals of a clone, or an inbred line. It is quite possible that one female can be responsible for an infestation of thousands and thousands of mites in a particular nest in a very short period of time since a considerable amount of inbreeding results. Many thoroughly inbred lines may result in any given locality and thus it is possible for the inherent variability of the genetic pattern to become apparent in the same area, just as it is possible to select or breed out many different strains of organisms by inbreeding. Host-specificity in these forms is largely a matter of nest-specificity. When these forms have been taken into the laboratory and bred under laboratory conditions, it is found that many hosts may be suitable. The condition of the nest is more critical than the species of host that is used to feed the parasite. The little we know of these forms indicates that they tend to have a wider geographical distribution than do those species whose breeding is quite independent of the host. This of course is what we should expect. Hosts pick up these mites and transport them from place to place. Whenever a host enters a suitable nest, the mites can reproduce in large numbers. Given a nest with certain environmental features favorable to the reproduction of the mites, it is quite possible that the mites will be found in the nest. Many of these species are holarctic in distribution. Except for those forms that are on domestic animals or are parasitic on the rodents parasitic on man, most species do not extend from pole to pole.

The third type of pattern among the parasitic mites is that in which the entire life cycle of the mites takes place within or on the host. Here interbreeding is even more restricted than it is among the nest parasites, and because of this extreme inbreeding we should expect to get more variation among the forms than is

found in parasites that live and breed in nests. Host-specificity in this group of mites has for many years been considered to be quite narrow, because morphological differences were reported among similar forms found on different hosts (Hirst, 1919). Of all the parasitic mites, the host-specificity is probably greatest here. It is comparable to the host-specificity of certain of the internal parasites that reproduce within their host. However, a number of these species have rather broad host ranges. They normally are transmitted from host to host only by close personal contact of the hosts, one with the other; therefore, when such close personal contact is provided, they will go from one host to another. Relatively little work has been done on host-specificity in these forms, and the obvious chore of describing the characteristics of these parasites as they occur on some of our more common animals, especially the domestic animals, is still to be undertaken. Recently it has been demonstrated that *Chorioptes*, a form that was formerly thought to be extremely host-specific and to be a polytypic species composed of many strains, each strain on a different host, is really not very host-specific at all (Sweatman, 1956). *Chorioptes* from cattle were found to be capable of living on epidermal scrapings from a number of other animals. The differences found in specimens of different populations of mites of this type may result from phenotypic manifestations produced by inbreeding, rather than subspecific differences associated with isolation resulting from partial or complete host-specificity.

To summarize, intraspecific variations in parasitic Acarina are produced by the same processes as are known to produce intraspecific variations in other forms. There are three main reproductive patterns among the parasitic Acarina. Those parasitic Acarina whose breeding activities are carried on in the free-living stages in the life cycle show intraspecific variation similar to that exhibited by other free-living forms, and such intraspecific variation could be recognized by the naming of the subspecies of the polytypic species that are known for this group of mites. On the other hand, those species of parasitic mites that carry on all of their life cycle, including their breeding, on their host have a type of intraspecific variation that one finds in highly inbred animals. Most variation seen in these forms is varietal rather than subspecific in nature. Intermediate between these two types are the parasitic acarines that live and breed in the nests of their hosts.

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G. W. WHARTON is Professor of Zoology and Chairman of the Department of Zoology, University of Maryland. Professor Wharton was President of the Society of Systematic Zoology during 1956.

Utilization of X-Rays as a Tool in Systematic Zoology

ROBERT RUSH MILLER

AS THE science of systematic zoology advances, its methods are becoming increasingly refined by the development of new tools or the improvement of existing ones. Practical use of X-rays in the field of systematics has been demonstrated repeatedly during the past fifty years, but radiography is still a relatively new and little-known tool to most such workers. Recent developments, such as soft-ray machines, stereoradiography and cinefluorophotography (X-ray movies), hold great promise for wider and more general use of X-rays by systematic zoologists as well as by others. The purpose of this paper is to discuss briefly different types of radiation, to point out the value as well as the limitations of these techniques, and to present data obtained from experiments with different types of X-ray machines.

"Hard Rays"

A demonstration of the practical application of radiography to biology was first published by Meek (1896), the year after Roentgen discovered X-rays. The type of radiation employed was the so-called hard rays, radiation of relatively short wavelength produced with high voltage, somewhat similar to those used today in ordinary medical work. Hard and soft, as applied to X-rays, are relative terms. When X-rays are produced at 50 kilovolts, for example, a wide spectrum of radiation results, including "soft" as well as "hard," or low-energy as well as high-energy, X-rays. For the purpose of this paper, hard rays may be considered as those produced at about 40 KV or higher.

The field of paleontology is one of the most fertile for the systematic application of hard rays, and students of fossil animals were the first to utilize and develop this tool advantageously on a broad scale (Schinz and Peyer, 1934; Lehmann, 1938; Zangerl, 1948; Kuhn-Schnyder, 1954). Many paleontologists have used radiographs as a guide to the preparation of delicate fossils, or as a substitute for preparation when the mechanical removal of the rock from the fossil could not be accomplished safely. Usable materials are limited by such factors as the comparative density of fossil and matrix and by the thickness of the matrix, which should not greatly exceed that of the fossil. Remains embedded in clays, bituminous or coaly shales, and diatomaceous earth yield excellent results.

By means of radiographs, students of extinct life—particularly faunas of Pliocene or Pleistocene age—can most advantageously compare suitable fossil forms with their nearest relatives. Whenever feasible, recourse to roentgenograms saves hours of tedious dissection of both fossil and Recent remains. Moreover, the illustration of such material in scientific papers makes these contributions far more meaningful than paragraphs of dry descriptive matter.

Stereoradiography

The use of three-dimensional radiographs, obtained by means of stereoradiography, has greatly broadened the application of X-rays to systematics. This technique overcomes a major disadvantage of conventional radiography, namely, that the relative positions of various parts

within the body, such as the bones of the head region, are obscured by the many overlying structures. The attainment of depth by means of X-ray stereographs seems almost to tear the superimposed layers apart, thus making it possible to interpret the individual elements much more readily, including even blood vessels and foramina. In order to produce roentgenograms that give true stereoscopic effects, two slightly different views are obtained that correspond to the different images seen by the two eyes. This is accomplished by taking two radiographs—one from each of two positions of the X-ray tube. The object to be X-rayed and the film remain in the same relative position during each exposure. After the proper amount of shift of the tube is determined, it is centered on the object and then shifted to one side one-half the total tube shift. When the exposure has been made, the tube is shifted an equal distance from the center in the opposite direction, the shift being kept parallel to the plane of the film. The same exposure and processing is given to each radiograph so that the two differ in appearance only insofar as the two positions of the X-ray tube produced a difference in the projected images. When the two films are properly viewed in a stereoscope, a three-dimensional effect is achieved.

Not only are the relationships between various structures greatly clarified with this technique, but fine detail appears to be more definite than in a single radiograph. Dr. Rainer Zangerl has perfected this method and has applied it effectively not only to fossil animals but also in studies of the comparative anatomy of Recent vertebrates. For practical purposes, however, stereoradiography is limited to sizeable animals. Nevertheless, by using very soft X-rays (see below) and photographic film, it is at least theoretically possible to obtain satisfactory stereographs of smaller organisms. A special type of stereoscope is used to study stereoradiographs, and the radiographs need to be placed in special viewing boxes. Sometimes it is advisable to overdevelop the sheets of metal and occasionally in mediviewing box in order to bring out maximum detail.

"Soft Rays"

The recent invention of the beryllium window X-ray tube has made it possible to obtain detailed radiographs of certain types of biological materials heretofore beyond the reach of the ordinary X-ray machine (Figs. 1–4). X-rays of many wavelengths are produced when electrons bombard a target of high atomic number. The shortest wavelength of the spectrum of X-rays is determined by the maximum accelerating voltage across the tube, whereas the longest wavelength is determined by the ability of the window to transmit low-energy X-rays. The selection of material of the lowest possible atomic number for a window permits the X-rays of longest wavelength to emerge and these, in turn, produce the highest contrast radiographs of relatively thin objects. As X-ray penetration is decreased by reducing the voltage and by using rays of longer wavelength, the relative absorption of delicate structures with different opacities will increase; hence, relatively low penetration will give maximum contrast. The thin beryllium window of low atomic number allows the passage of soft X-rays of relatively long wavelengths, under low voltages, and insures a minimum filtration between the X-rays' source and the film. Beryllium allows the soft radiation to pass through the window and thus makes it possible for a soft-ray machine to produce results that cannot be obtained with a hard-ray unit. These low-energy X-rays are the type used in the metal-casting industry to detect flaws in thin sheets of metal, and occasionally in medicine for superficial skin therapy; more recently, they have been utilized in grain inspection units to reveal insect infestation inside of wheat kernels and similar foodstuffs.

In addition to revealing structures as delicate as the veins of leaves, soft rays also give greater clarity to thicker parts

(up to thicknesses which they can penetrate) than do the short-wave, high-voltage rays. High-contrast radiographs are obtainable with Type M film, but the outstanding advantage of the soft-ray machine is that photographic film can be substituted for X-ray film. Contact prints or enlargements made from photographic film are far more satisfactory for scientific illustration or for teaching purposes than are reproductions made from X-ray film. X-ray film has an emulsion on each side, whereas photographic film is coated on one side only; this accounts for the difference in photographic clarity.

There is less latitude in determining correct settings and exposures with soft-ray than with hard-ray machines, but the increased detail obtained justifies the additional time required for experimentation. Soft rays enable one to distinguish, for example, between cartilage, calcified cartilage and bone.

Cinefluorophotography

One of the latest developments in the application of X-rays has been the so-called X-ray movies, more properly called cinefluorophotography because they are photographs of an image on a fluorescent screen rather than the direct effect of X-rays on film. The following example of the application of this technique was received from Dr. James A. Oliver of the New York Zoological Society. For a long time it was maintained that in rectilinear or caterpillar locomotion snakes literally "walked on their ribs," since it was believed that the ribs, rather than the skin, moved forward and backward. By cutting a small window in the skin, two scientists had determined that it was the skin and scales that moved, but this test did not serve to convince all workers. X-ray movies of an African puff adder performing this type of locomotion provided a vivid, convincing demonstration that the skin and abdominal scales, not the ribs, are the responsible motivating force. These movies are incorporated in an educational film on snake locomotion released by the Society.

The dosage used in making a cinefluorophotograph of a large African lizard (*Agama*) was about 60 roentgens, measured in air. While the technique may contribute to the advanced death of the subject, the movies are a promising tool in many kinds of studies.

Topographic Radiography

Very recently Richards (1956*a*) has developed a new and potentially valuable radiographic technique that utilizes liquid and solid radiopaque molds and replicas to show surface features—whence the name, topographic radiographs. The method can be applied to nonhomogeneous radiolucent or radiopaque objects of any thickness that have details on one or more surfaces, and these surfaces need not be flat. By immersing an object such as a leaf in a radiopaque liquid, an image can be obtained on radiographic film by conventional exposures and machines. A small quantity of a saturated solution of zinc bromide (447 gr. of $ZnBr_2$ dissolved in 100 gr. H_2O) is placed on a thin sheet of cellulose acetate, the leaf is positioned on this pool of liquid, and then more radiopaque fluid is deposited on top of the leaf. Next a second thin sheet of cellulose acetate is laid over the second quantity of liquid, thus forming a "sandwich" which is then placed on radiographic (dental) film and the X-ray beam directed perpendicularly to the plane of the film. The thin layer of zinc bromide that is trapped between the leaf and the acetate sheet nearest to the film forms a faithful radiopaque mold of the leaf surface on one side and of the flat surface of the plastic sheet on the other. The variation in thickness of the liquid mold is responsible for the differential absorption of the X-ray beam to form the image on the film. Elevations appear dark and depressions light in topographic radiographs of radiolucent objects and the reverse is true for some radiopaque objects. Details of one or the other surfaces of such an object, or of both surfaces simultaneously, may be reproduced; a radiolucent barrier, such as pe-

troleum jelly, is used to prevent the formation of an impression of the undesired surface. The film used in making topographic radiographs is radiatized dental film; the settings are: 40 KVP, 6 MA, at a distance of 10 inches and an exposure of 4 seconds, using a conventional dental unit X-ray machine.

The relationship of surface configurations to underlying structure, such as scale number to vertebral number, can be detected effectively with this technique. It has also been of demonstrated value in paleontology and archaeology, and can reveal the inner surface configuration of tubes and the wing venation of insects. The method should prove of considerable aid in rendering a drawing that involves accurate reproduction of surface detail. Details of the topography of a concave surface, frequently difficult to illuminate properly by photography, can be readily depicted by liquid molds with the aid of a toy balloon that presses the radiopaque liquid evenly over the concave surface (Richards, 1956*b*).

Value and Limitations

The value of X-rays in systematic studies has been shown for both invertebrates and vertebrates, for example in ichthyology (Gosline, 1948; Bonham and Bayliff, 1953). As pointed out earlier, vertebrate paleontologists have benefited particularly from this tool, especially during the past 25 years. The speed of the method and the greater availability of taxonomic materials (Johnson, 1955*b*) are among the outstanding advantages of radiography. With the recent development of soft-ray units, the substitution of photographic film for X-ray film has greatly widened the usefulness of X-ray photography. For the rare or type specimen, there is no substitute for roentgenograms if a knowledge of internal structure is required for identification or for determining relationships.

X-rays may reveal food habits (Parker, 1955) and thus supply data of value to the student of the prey as well as of the predator. For example, mollusks eaten by fishes may reveal new data on ecology and distribution for the conchologist as well as the food preference of the fish (Miller, 1955, p. 50). Skeletal abnormalities are readily discerned (Fig. 3*B*; Breder, 1954, Pl. II) and may be verified when some other external manifestation indicates a probable deformity (Follett, 1954). Comparative osteology and to some extent comparative anatomy are particularly amenable to study with this technique. It is practicable to survey rapidly a group or groups of related species (genus or family) to ascertain what internal structures may prove to be of importance in their classification (Nelson, 1948, p. 233; Tucker, 1953); many tedious days of careful dissection may thus be avoided. In studying the correlation between lateral musculature and swimming in fishes, Nursall (1956) utilized radiographic analysis to aid in interpreting skeletal relations. In working out cranial osteology, Eigenmann (1927, Pls. V-VI) relied upon roentgenograms to supplement drawings.

The method also makes possible the study of variation, a central theme of systematic work, through the analysis of long series of specimens. The most obvious advantage of radiography in ichthyology and fishery research is the study of vertebral variation at taxonomic levels from race to family (Bailey and Gosline, 1955). Not only are specimens uninjured but such counts are determined with greater speed and accuracy than when dissection is employed. Use of photographic film (or even Type M X-ray film) with soft radiation makes possible the ready application of X-ray photography for teaching purposes by use of enlargements and lantern slides. The technique is also very helpful for scientific illustration when a drawing is preferred, since the artist may readily overcome the slight but annoying inaccuracies that all too often appear on figures of new taxa. A radiograph should also speed the time required to complete an illustration through the rapid and accurate establishment of points of reference. This tool may also

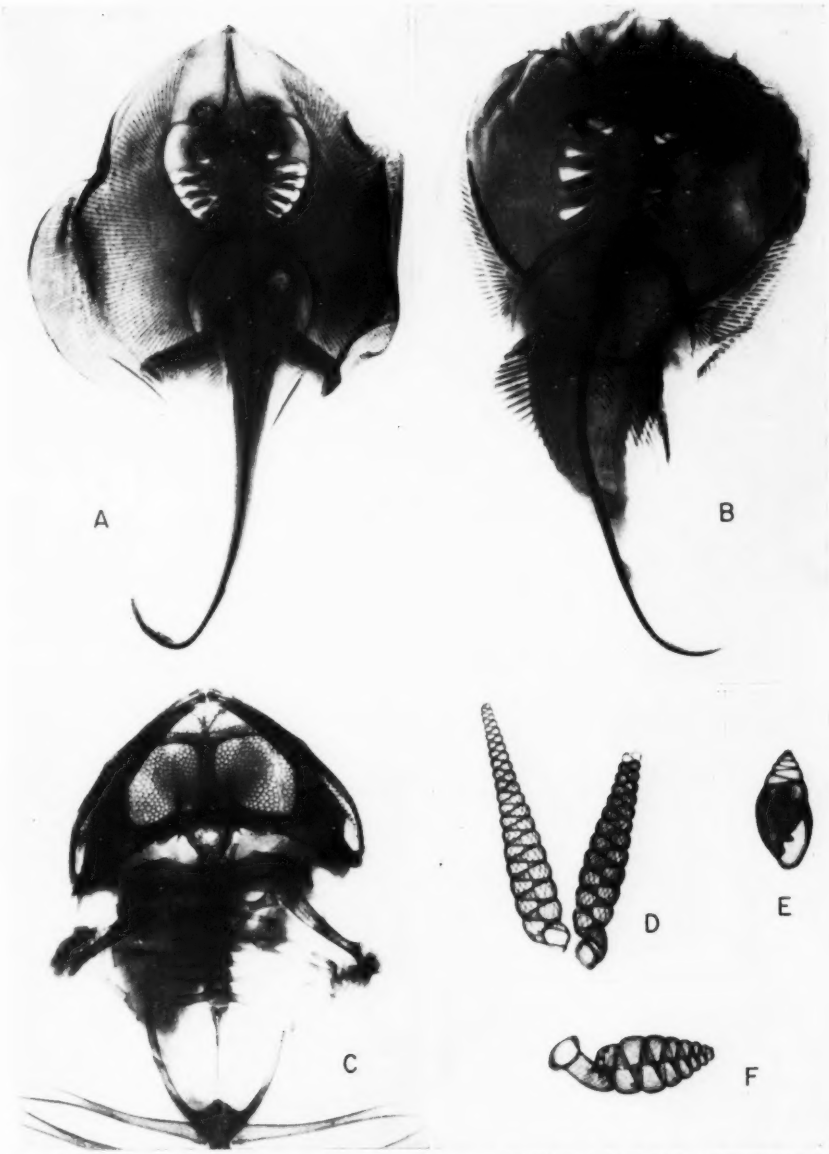

FIG. 1. Radiographs with two soft-ray machines at 25 KVP, 5 MA, 20 inches. *A, Raja fusca* (UMMZ 142874), 62 mm. disk length, from Japan; Maximar 100, 1:45 sec. *B, Narcine brasiliensis* (UMMZ 155027), 57 mm. disk length, from Florida; Model F–5, 4 min. (For other detailed radiographs of rays, see Bigelow and Schroeder, 1948: Figs. 1–2.) *C, Hemiphractus* sp. (UMMZ 57528), maximum skull width 47 mm, from South America; F–5, 18 min. *D, Brachypodella spelluncae* (UMMZ 64539), total lengths 10 & 12 mm., from Guatemala; Maximar 100, 1:30 sec. *E, Phytia setifer* (UMMZ 114765), 11 mm. long, from California; as above. *F, Holospira hinkleyi* (UMMZ 142241), 8 mm. long, from México; as above.

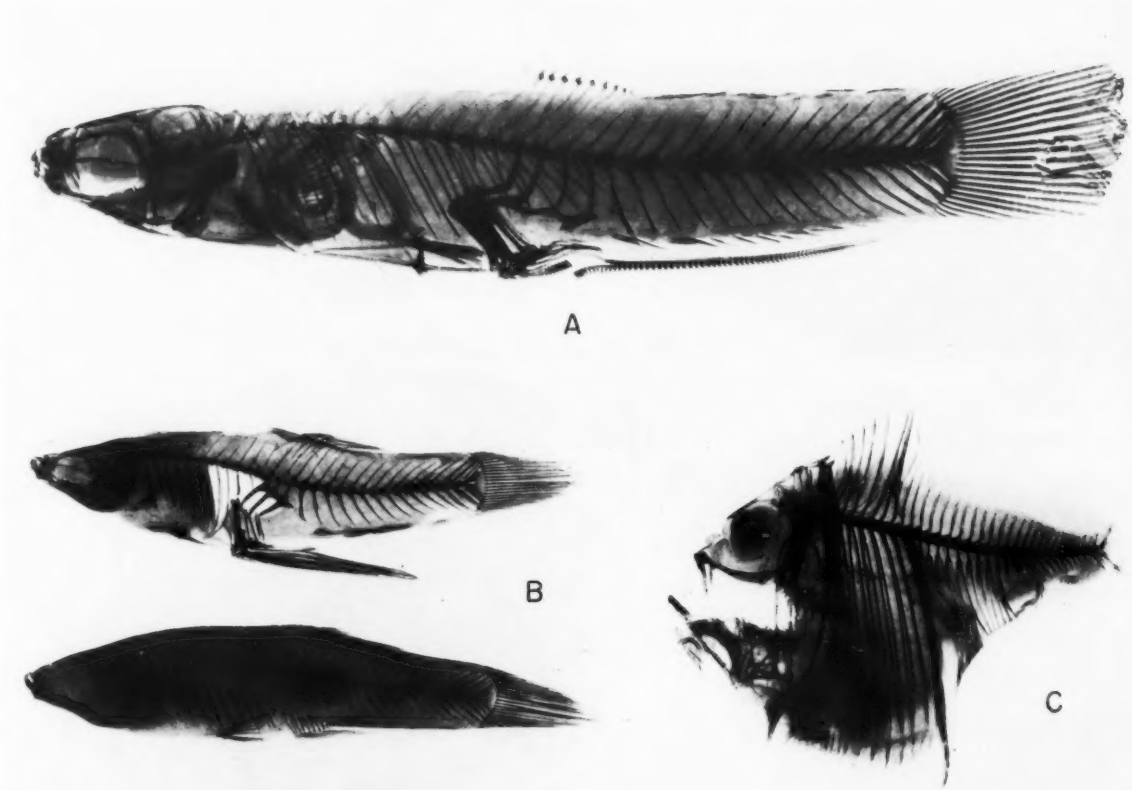

FIG. 2. Radiographs with two soft-ray machines at 25 KVP, 5 MA, 20 inches. *A*, Holotype of *Xenodexia ctenolepis* (UMMZ 105460), 40 mm. standard length, from Guatemala (compare with Hubbs, 1950; Pl. IV, Fig. 1); Maximar 100, 2:20 sec. *B, Dactylophallus denticulatus* (UMMZ) 108683), male (above) 34 mm. and female (below) 35 mm. long, from Cuba; Model F–5, 4 min. (This and the preceding species are viviparous.) *C, Argyropelecas aculeatus,* a deepsea hatchet fish 37 mm. long, from Bermuda; F–5, 6 min. Note photophores (light organs).

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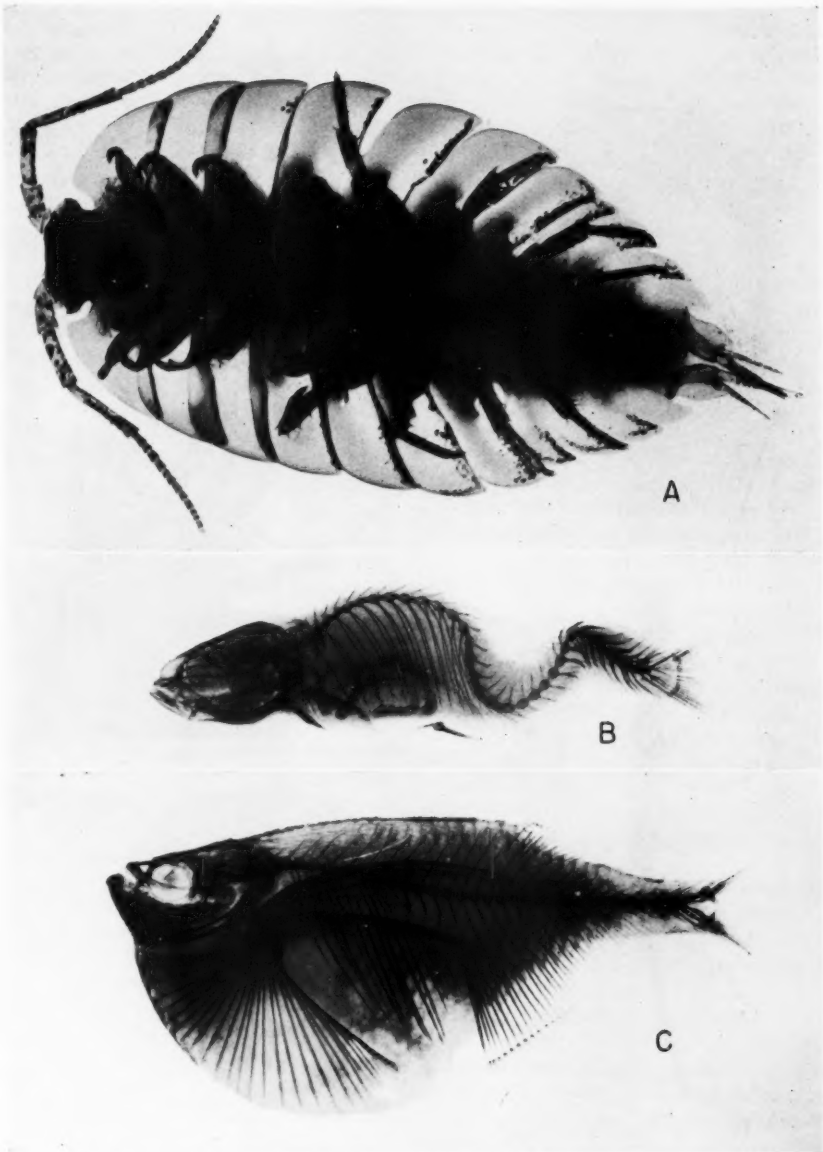

FIG. 3. Radiographs from two soft-ray machines taken at 25 KVP, 5 MA, 20 inches. *A*, An isopod 45 mm. in total length, from Washington; Maximar 100, 2:30 sec. *B, Chrosomus eos* (UMMZ) 167947), 41 mm. long, from Michigan; Model F–5, 5 min. *C, Gasteropelecus* sp., 55 mm. long, from Peru; Model F–5, 6 min. Note enlarged pectoral girdle for muscle attachment associated with flight.

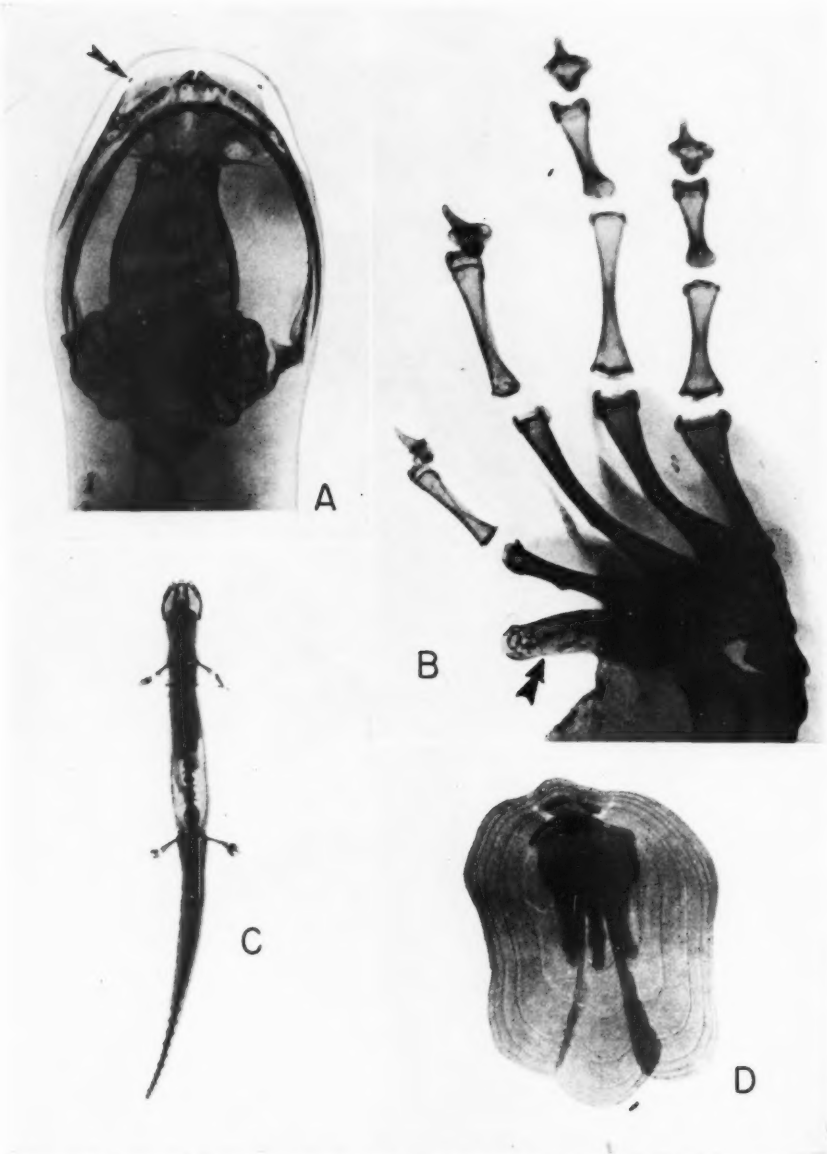

FIG. 4. Radiographs from two soft-ray machines at 25 KVP, 5 MA, 20 inches. *A*, Head of *Chiropterotriton mosaueri* (UMMZ 88841), enlarged about 8.5 times, from México; Model F–5, 5 min. Arrow points to septomaxilla bone; slightly retouched. *B*, Right foreleg of *Plectrohyla* sp., from México, enlarged 6 times, to show pre-pollux (arrow); F–5, 4 min. *C*, *Bolitoglossa odonnelli* (UMMZ 89101), from Guatemala, actual size; F–5, 5 min. *D*, Greatly enlarged scale of northern pike, *Esox lucius*, in ninth year of life; Maximar 100, 1:45 sec.

be applied to life-history work by injecting radiopaque substances into small vertebrates as a marking technique; such tracers do not harm the organism and may be quantitatively retained by the animal practically throughout its life (Hasler and Faber, 1941).

Microradiography of microfossils (Schmidt, 1952), or of such minute organisms as ostracods and Foraminifera, has been accomplished recently by the use of X-ray diffraction equipment. This method is valuable for the study of whole specimens as well as of thin sections; internal structures of taxonomic importance can be detected, thus making unnecessary the tedious and destructive technique of grinding out sections of these organisms.

The internal sculpturing of certain mollusks (Fig. 1*D–F;* see also Moore, 1955) —a feature of taxonomic value otherwise visible only by destroying part of the shell—may readily be revealed with soft radiation. In his unpublished studies of the comparative morphology of the trachea of ducks and their allies, Dr. Philip S. Humphrey has found hard rays useful in facilitating the rapid and accurate enumeration of tracheal rings and in working out the relationship between these rings and the overlying musculature; the tracheal rings and their various fusions and expansions are of value in determining broad relationships in these birds.

Certain osteological features of amphibians, reptiles and mammals have proven to be amenable to study with both hard and soft X-rays, and details of skeletal specializations in small fishes and amphibians (Figs. 2, 4) are revealed by soft rays. The septo-maxilla, a minute paired dermal bone, is important in the classification of the plethodontid salamanders but is so tiny as to be missed in ordinary skeletal preparations; this bone is readily revealed by low-energy X-rays (Fig. 4*A*). The prepollux is a bony digit found only in males of certain frogs; its shape is utilized in distinguishing species of *Plectrohyla,* and an accurate illustration of the digit (Fig. 4*B*) is greatly facilitated by radiography.*

Radiographs have also been useful in verifying the taxonomically important costal-groove count of salamanders by providing a ready means for counting the number of rib-bearing vertebrae between the skull and the pelvis. Also, the soft anatomy of these and other animals may be revealed by low-energy radiation (Fig. 4) and may thus become available in working out relationships.

A major limitation of X-ray photography as applied to systematics is that many biological materials are not suitable and others cannot be used for practical reasons. The technique is not intended as a substitute for the preparation of skeletons or for clearing and staining, both of which will often be necessary. Clearing and staining, however, is a tedious process; the materials so treated must be stored in glycerine, and the technique is undesirable for type or rare specimens. Thus far, X-rays seem to offer no particular help to the systematic entomologist, although pictures of the venation of beetle elytra and of lepidopteran wings may be of value. The application of the technique is still in the experimental stage and wider use of X-rays, along with greater refinements and advances in machines and in techniques, may be expected to broaden their utility in systematics. The method represents a most promising tool for taxonomic analysis.

Costs of equipment are no longer prohibitive. A soft-ray machine (Model F-5, General Electric Co., see below) may be obtained for about $1500 (including protective housing), and a good, used conventional voltage machine costs about $500. Type M X-ray film, 7 × 7 inches, is approximately 45 cents a sheet and photographic film, 8 × 10 inches, amounts to 20 cents a sheet. X-ray units are now being used for systematic work in at least 13 educational institutions in the United States and Canada, in a number of the

* I wish to thank George B. Rabb, doctoral student at the University of Michigan, for the foregoing information on the septomaxilla and pre-pollux.

large museums of Eurasia, and at the C. S. I. R. laboratory in Australia.

Machines, Exposures, and Processing

The hard-ray machine in use at the University of Michigan Museum of Zoology is a GE hospital bedside unit (see photograph, opposite p. 18, in Rept. Director Mus. Zool. for 1946-47, published in 1948). It was purchased in 1947 from the War Assets Administration for $65 (original cost about $1300) and was manufactured by the General Electric X-ray Corporation, Chicago (Model D type). No intensifying screens or filters are used. This machine gives good results for radiography of small vertebrates (about 1 to 16 inches long and up to several inches thick) and suitable invertebrates (snails, starfish, etc.), where fine detail is not required. By using industrial Type M X-ray film (Eastman Kodak Co.), which is fine-grained and gives high contrast, satisfactory detail is discernible on smaller specimens and greater clarity is obtained with larger organisms. Medical film (Blue Brand, Eastman Type F) does not yield usable radiographs for small specimens because the grain is too coarse and the contrast too low, so that when the film is magnified, structure merges into grain and is lost. With Type M film, details become obscure only on small, relatively thin objects (such as a trout less than one inch long). For some purposes, however, as in interpreting muscle distribution relative to the skeleton in an animal of cat size, medical film is satisfactory and has the advantage of a much shorter exposure time. Type M film requires an exposure about seven times that of medical film and is somewhat more expensive (45 versus 35 cents a sheet 7×7 inches). As in all radiographic work, the shorter the exposure the less the latitude in exposure time.

The target-film distance (between the focal spot of the tube and the film) found to be most satisfactory with the machine described above is about 32 inches at an exposure of 33 seconds using about 65 KVP (peak kilovolts). Generally speaking, the greater the distance between focal spot and film, the sharper the resultant detail in the radiograph, but the exposure must be longer. Specimens to be X-rayed are placed directly on a lead-backed film holder, which is covered by a thin sheet of plastic for material preserved in liquids. The shorter the object-film distance, the greater the detail and the less the magnification or distortion (Johnson, 1955*a*). The autotransformer is set at the lower range, usually 2, and the milliamperes (MA) are maintained as closely as possible to 10. No cones or cylinders are used, since no fogging from secondary radiation is apparent. No one is in the same room as the machine when it is being operated. These details will vary with different machines and materials, but with Type M film the same exposure time can be used with apparently equal effectiveness for rather flat fishes from about 1 to 7 inches long. However, for large, thick specimens (such as those shown in Hubbs and Miller, 1953, Pl. III), the setting on the autotransformer should be advanced (in this example to 3), in order to increase the penetration of rays, and either the exposure time or the milliamperes should be increased (in the above case exposure time was increased from 33 to about 60 seconds), in order to obtain sufficient definition. Raising the milliamperes results in the production of more X-rays. No change in the target distance was found to be necessary with the larger specimens.

In his work on fossil reptiles, using medical (Blue Brand) X-ray film, Dr. Zangerl applied 50 KVP at 5 MA and 30 seconds exposure at a target distance of 42 inches to photograph a fossil embedded in coaly shale (Zangerl, 1948, Fig. 2). In X-raying a Recent, large stingray, he varied the above settings only by changing to 3 MA.

The soft-ray roentgenograms shown in Figures 1 to 4 were obtained with a General Electric Maximar 100 X-ray unit and also with a GE Special Model F-5 machine (the latter is housed in a specially constructed, lead-lined box). Each of these machines has a berryllium-window

tube and tungsten target. Both X-ray film (Type M) and photographic film (Super-ortho Kodalith, made by Eastman) can be used, but the latter is preferred if prints are to be made. The specimens were placed directly on top of thin, black photographic (light-proof) paper that contained the X-ray or photographic film; material preserved in liquid was placed on a thin sheet of plastic overlying the paper. When standard cardboard film holders were used, the fibers in the cardboard appeared on both types of film. Best results on Type M film (with the Maximar 100 unit) using small, thin-bodied vertebrates 1 to 2 inches long, were obtained as follows: subject 33 inches from tube, 30 KVP, 5 MA, at an exposure of 20 seconds. For thicker-boned animals, such as small frogs and turtles around 2 inches long, an exposure of 2 to 2½ minutes was necessary at a target distance of 30 inches, 25 KVP, and 5 MA. At the same settings, exposures of 1¾ to 2¼ minutes were required for lizards about 5 to 7 inches long.

The following settings gave the most satisfactory exposures with photographic film. When fishes, amphibians, and snakes about 1 to 2 inches long were X-rayed, they were placed 20 inches from the focal spot of the tube, using 25 KVP and 5 MA, at exposures of 2 to 2½ minutes on the Maximar 100 and 3 to 6 minutes on the F-5 model. The small, thin-bodied sting-ray (disk-length about 2½ inches, Fig. 1 *A*) required an exposure of only 1¾ minutes (Maximar), and the somewhat thicker one (Fig. 1*B*) 4 minutes (on the F-5 model). For somewhat larger and thicker fish, 3- to 10-minute exposures were necessary at these settings. Small snails, 8 to 12 mm. long (Fig. 1*D-F*), needed an exposure of only 1½ to 2½ minutes or, using settings of 12 inches, 30 KVP, and 5 MA, an exposure of about 30 seconds was required on the Maximar 100 machine.

Processing either X-ray or photographic film is readily accomplished in an ordinary dark room. The only special chemicals needed are X-ray developer (concentrate) and X-ray hypo. Since the sensitivity of both film types allows the use of a red light, developing can be done "by eye." The films are left in the developer not less than 5 minutes nor more than 8 minutes, except that photographic film may be left in as long as 10 minutes (no fogging) if desired. Reasonable temperature control enhances the developing of photographic and X-ray film. Note that X-ray rather than photographic developer is used to develop photographic film; when D-85 Kodalith developer was tried, results were poor.

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ROBERT RUSH MILLER is Curator of Fishes in the Museum of Zoology, and Associate Professor of Zoology, University of Michigan. A preliminary report on the subject of this paper was given at the meetings of the Society of Systematic Zoology in St. Louis, December 1952.

Spread Potential and the Colonisation of Islands

DENNIS LESTON

OCEANIC island faunas usually are analysed by division into groups emanating from various zoogeographical areas. Such a division has been done for the 43 bugs—Hemiptera Heteroptera—of the Açores (data of Leston and Carthy, 1957), an example uncomplicated by endemism (Fig. 1). The information given may be considered a product of past and present geographical position and available ecological vacancies. Little indication of the ability of a taxon to migrate, or of its colonising potential, is given by this method but, it is suggested, a technique is applicable which evaluates these hidden factors.

The Heteroptera of Islands

Zimmerman (1948) lists 223 species of bugs in the Hawaiian archipelago, with 80 per cent endemism. The native forms can be arranged in a limited number of monophyletic blocks (Table I). Thus the 17 species of Pentatomidae *sens. lat.* (Pentatomoidea of many authors) comprise two immigrants, an isolated endemic and 14 other endemics, the last-named the descendants of a prototype *Oechalia* which subsequently speciated explosively: the two immigrants and the two hypothetical prototypes add up to four species known to have reached the island from an outside source, to have been able to colonise, and to have survived in changed or unchanged form (minor changes in the genotype are not relevant to the present analysis). Whether a species has been introduced by man or other biological agents is also irrelevant in the present context. The Lygaeidae of Hawaii, 83 species, comprise eight immigrants, three endemics from one proto-

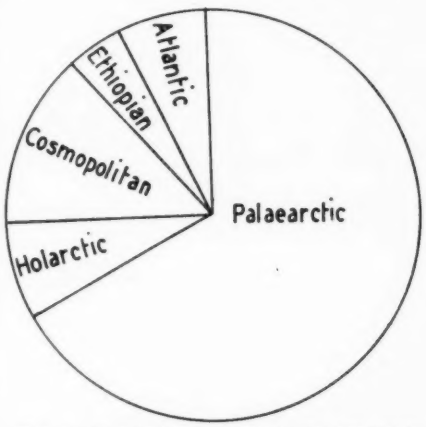

FIG. 1. Faunistic analysis of the 43 species of Hemiptera Heteroptera of the Açores. Atlantic = Maderia and/or Canaries.

TABLE I—IMMIGRANT AND ENDEMIC SPECIES OF SOME FAMILIES OF HETEROPTERA IN HAWAII

GROUP	IMMIGRANT SPP.	ENDEMIC SPP.	MINIMUM NO. HYPOTHETICAL PROTOTYPE SPP.
Pentatomidae	2	15	2
Alydidae	0	2	1
Rhopalidae	1	0	0
Lygaeidae	8	75	2
Tingidae	1	0	0
Emesinae	6	1	1
Reduviidae	2	0	0
Nabidae	1	24	1
Anthocoridae	6	6	1
Cimicidae	1	0	0
Miridae	9	29	7
Cryptostemmatidae	1	0	0

Data from Zimmerman, 1948; the last column gives the minimum number of prototype immigrants which can be postulated as ancestral to the endemic species.

type and 72 endemics from another prototype—in this case a *Nysius* species.[1] This family scores 10. The histograms (Fig. 2) show the known heteropterous faunas of Açores (no corrections needed for endemism), Hawaii, Guam (data from Usinger, 1946) and Samoa (data from China, 1930; Knight, 1935) treated in like manner: the divisions into taxa are an arbitrary choice dictated by the nature of the available information.

Comparison of the Island Faunas

Bug collecting on the four island-groups has not been of equal intensity but the histograms expose an unexpected similarity between the immigrant faunas of Açores and Hawaii and, less markedly, between these, Guam, and Samoa. The first 12 groups—Pentatomidae to Nabidae—are represented in Portugal by the following numbers of species respectively: 95, 27, 5, 11, 4, 2, 102, 7, 25, 2, 20 and 9 (data of Seabra, 1941). These figures show that the Açores fauna, although demonstrably originating mainly from Portugal, is not merely an improverished but representative sample of that of the nearest mainland: the absence of Coreidae and dominance of Emesines over other Reduviidae are noteworthy in this respect. On all major land-blocks there are far higher proportionate numbers of Pentatomidae, Coreidae, Reduviidae and Hydrocorisae than are found on the island-groups under discussion.

That oceanic island faunas have many lacunae has been appreciated since the days of the pioneer zoogeographer Wallace, but the histograms demonstrate a similarity in gaps, peaks and the relative heights of peaks. The features already noted in the Açores fauna are duplicated in Hawaii; tingids are represented by a single species—in each case a different one—on the four archipelagoes; Cimicidae by a single species on each. The relative abundance of many families, measured in terms of immigrant and prototype species together, is closely similar on the four island-groups: this can be shown by scoring 1, 2, 3 *et seq.* for the taxonomic groups in descending order (Table II). The single obvious irregularity is the small score for the Samoan Anthocoridae, but there is some evidence to suggest that this family has been overlooked by taxonomists working on the Samoan fauna.

The relative positions—expressed in the last column on Table II as a fraction of the mean mirid score, but susceptible, if required, to analysis by the Rank Coefficient statistical technique—cannot be a mere reflection of geographical criteria: the four island-groups are in different oceans, different latitudes and adjacent to different continents or archipelagoes, whilst the migrations and mercantile activities of man differ greatly in form and intensity between, say, Hawaii and Guam. As for the possibility that the availability of ecological niches has influenced the relative positions, this has largely been eliminated by the analytical method used: subsequent post-colonisation speciation has been deliberately cut out of the figures utilised. Hence the numerical values obtained are a *relative consequence of*

TABLE II—RELATIVE POSITIONS OF THE FIVE PRINCIPAL GROUPS

	AÇORES	HAWAII	GUAM	SAMOA	MEAN
Mirids	1	1	1	1	1.0
Lygaeids	2	2	2	2	.5
Pentatomids	4	5	3	3	.3
Emesines	4	3	5	4	.3
Anthocorids	2	3	4	8	.2

The mean position is expressed as a fraction of the mean value for mirids.

[1] Mayr (1942) repeats Usinger's assertion (1941) to the effect that the 72 species treated here as being monophyletic are not so. Examination of the complex in the works of Usinger and Zimmerman and the scanty British Museum (Nat. Hist.) material leads me to believe that the complex is monophyletic and has not been augmented by later immigration by stepping stone routes: however, even if Usinger is correct it scarcely affects the thesis developed here.

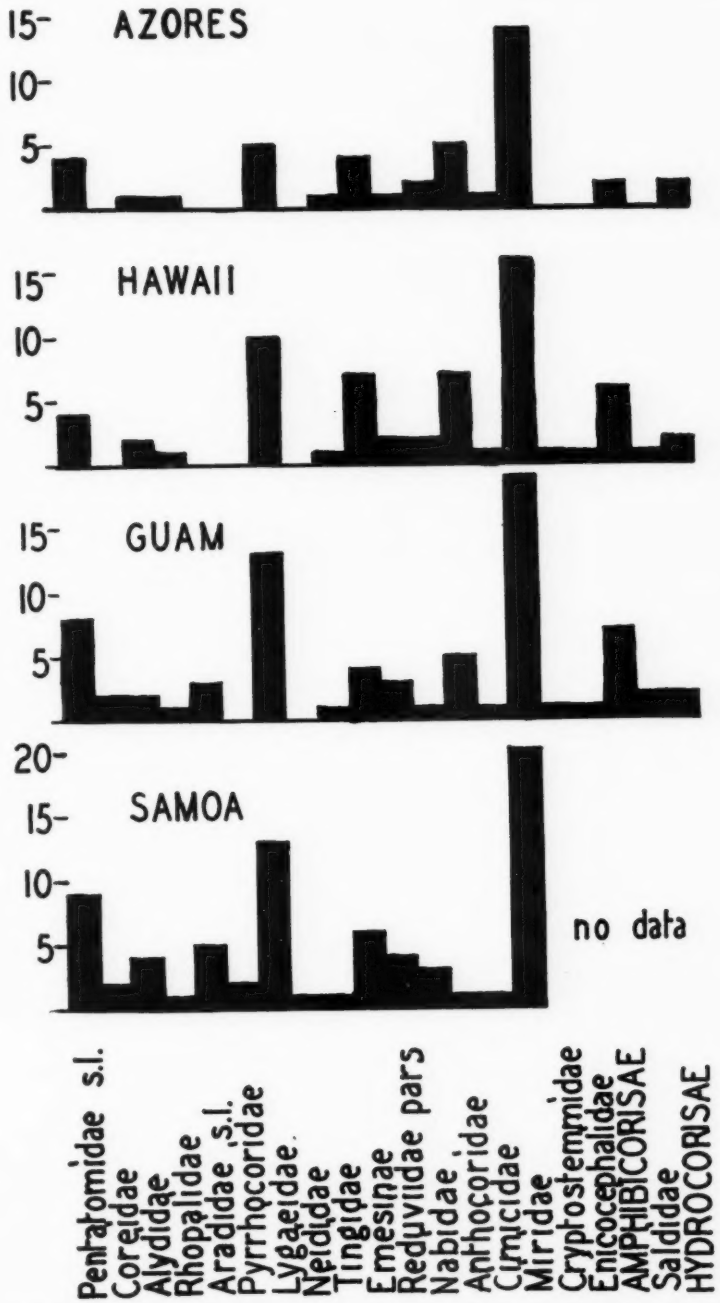

FIG. 2. Histograms of the numbers of immigrant and prototype species of four oceanic island groups. N.B. Pentatomidae is used in the widest sense, Pyrrhocoridae includes Largidae, Aradidae is used in the widest sense, Reduviidae are divided into Emesinae and the rest.

properties intrinsic to the taxa. Differences in age between two islands would show in a general increase or decrease of representation by all families rather than by a selected few, were there no intrinsic group differences.

Spread Potential

The relative positions of the families as calculated so far merely show that some groups have a greater intrinsic ability to spread and colonise than certain other groups do. By working from the figures given in the histograms the mean number of immigrant plus prototype immigrant species can be calculated, based on the four archipelagoes studied, for the various taxa represented in the faunas (Table III). Standard deviations are in some cases excessively large because n is so small, but it is nevertheless felt that the means have a value, albeit an approximate one, as an indication of the relative spread and colonising ability intrinsic to the taxonomic groups. The relative values of m can be expressed as a percentage of the value for the top taxon, in this case Miridae: the value so obtained is styled the Spread Potential (SP).

TABLE III—SPREAD POTENTIAL, SP (EXPRESSED AS A PERCENTAGE OF THE SPREAD POTENTIAL OF MIRIDAE)

	n	m	SD_m	SP
Miridae	4	17.3	2.8	100
Lygaeidae	4	10.3	3.8	60
Pentatomidae	4	6.3	2.6	36
Emesinae	4	5.3	1.5	30
Anthocoridae	4	4.5	2.5	26
Reduviidae	4	2.5	1.3	15
Alydidae	4	2.3	1.3	13
Nabidae	4	2.0	0.8	12
Aradidae	4	2.0	2.4	12
Cimicidae	4	1.0	0	6
Rhopalidae	4	1.0	0	6
Tingidae	4	1.0	0	6
Coreidae	4	1.0	1.2	6
Pyrrhocoridae	4	0.5	1.0	3
Neididae	4	0.3	0.5	1

n, number of island groups sampled; m, arithmetic mean of the total of immigrant and prototype species; SD_m, standard deviation of the mean. N.B. Standard error of the mean is half the above standard deviations ($\sqrt{n} = 2$).

Spread Potential is a relative measure of the ability of taxa to migrate and colonise: the latter factor is, of course, to some extent dependant upon sufficient numbers migrating at any one time to permit foundation of a self-perpetuating breeding population. The arithmetic used can be put into a formula:

$$SP_t = \frac{100.\,\Sigma\,(s_{it} + s_{pt}).\,n_k}{\Sigma\,(s_{ik} + s_{pk}).\,n_t}$$

where s = number of species
n = number of islands or archipelagoes
t = taxon under investigation
k = standard taxon
i = immigrant species
p = prototype species

In fixing upon a group as standard, then

$$(s_{ik} + s_{pk}) > (s_{it} + s_{pt})$$

The Spread Potential formula can be expressed in other ways but remains a comparative diversity index. The statistical value or accuracy of a calculated SP is, of course, related to the value of the standard deviation: thus the value for Anthocoridae in the present instance is less accurate than that for Emesinae (Table III). Only by more intensive collecting and analysis of a greater number of island faunas can the accuracy of SP values be increased.

One immediate use for SP values is in providing an indication of taxa which in some areas may have been under-collected. They also indicate the quality of immigrants which may be expected to colonise an isolated land-mass.

Spread Potential of Heteroptera

The high SP of Miridae is what one would expect knowing the great numbers of these which are caught in light-traps, bearing in mind that light-traps are selective in that they catch only such insects whose behavior is not inimical to capture by this method. The numbers of species recorded by Thomas (1938) as

caught in four years trapping in southern England are: Miridae 57, Hydrocorisae 6+, Nabidae 3, Anthocoridae 2, Lygaeidae 2, Pentatomidae 2, Piesmidae 1. Families known to occur in the area but not recorded by Thomas include Reduviidae (with Emesinae), Aradidae and the series Amphibicorisae. The somewhat incomplete light-trap data of Frost (1952) also show Miridae to be numerically strong migrants.

The SP for Lygaeidae is surprisingly large until it is remembered that Orsillini genera extend to Iceland and are found near the tops of isolated African peaks. Another lygaeid, *Lygaeus equestris,* is known to reach Britain from the continent from time to time although it is unable to become established (Southwood and Leston, in prep.). The value for Pentatomidae is probably too large but a few species, e.g., *Nezara viridula, Aethus indicus* and *Geotomus pygmaeus,* are known to spread rapidly, perhaps with man's unwitting assistance. The value for Emesinae is unexpectedly high and out of all proportion to the representation of the group on continental land-masses: however, the biology of the group is but little understood. The comparatively static groups, Tingidae, Coreidae, Pyrrhocoridae and Neididae, give no explanation in their biology: *Pyrrhocoris apterus* is known to migrate some *Dysdercus* spp. (Pyrrhocoridae) may get transported with cotton and all four families are predominantly fully winged.

Discussion

Usinger (1941) sugested that the Hawaiian fauna may have, in part at least, reached the islands by stepping stones. The present work shows that anything the Hawaiian fauna may have, at family level, in common with other faunas (Usinger suggests New Zealand and Juan Fernandez amongst his examples) is due to some groups having greater or lesser Spread Potentials than others; of course at generic level an oceanic island may show similarities or even identities with nearby areas or along trade routes. However, it has been shown that Hawaii and Açores are almost identical in the composition of their basic fauna at family level, although this is masked by riotous endemism in the former: no floating continents, land bridges, lost island chains or trade routes have, to date, been postulated as connecting these two archipelagoes.

The present work has been based entirely upon the Heteroptera. Spread Potential is capable of universal application but it should be stressed that evaluation can only be carried out by competent workers with specialist knowledge of the groups under analysis: erroneous interpretation of the taxonomic data over the point "monophyletic or polyphyletic" would lead to valueless results. There is no reason why Miridae should not be taken as a standard for comparison with groups as diverse as birds or flatworms but in practice it will probably be found useful to adopt a numerous group of well-collected insects such as can be found in Lepidoptera or Coleoptera.

Summary and Conclusions

1. Analysis shows that, after reduction of the endemic species to their ancestral prototype species, the numbers of species which have reached certain oceanic archipelagoes and colonised them show a marked similarity for a given taxon on each island group.

2. The relative number of species of each taxon reaching an oceanic island reflects a property of the taxon rather than past or present geographical factors.

3. The relative ability of a taxon to spread and colonise is defined as its Spread Potential and a formula is given for its calculation.

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DENNIS LESTON, of 44 Abbey Road, London, N.W. 8, wishes to acknowledge the assistance of Dr. C. G. Johnson (Rothamsted Experimental Station) and Dr. T. R. E. Southwood (Imperial College, London) who have kindly read and criticised this manuscript. They are in no way responsible for any errors of fact or misinterpretations which may be found.

A recent letter from Dr. Zoltan Kaszab of the Hungarian National Museum carries the depressing news that the buildings, collections and libraries of the zoological section suffered disastrous damage in October and November. The Palaeontology and Mineralogy sections also suffered great destruction. Among the zoological exhibitions lost was the African Diorama, 25 meters long and modern in workmanship. More serious losses, scientifically regarded, are: 30,000 herps; 10,000 fishes; 40,000 birds; 30,000 eggs; 500,000 molluscs; mammal bones, including the African material of Kittenberger. The insect collections were also damaged, especially the Diptera section, in which 250,000 specimens (including 1000 types), 1500 volumes and 6000 separates were burned.

Dr. Kaszab writes that the museum *Annals* will probably be published this year, as usual, but includes in his letter the following (in a free translation): "The replacement of the destroyed collections and renewal of scientific work in the museum surpasses our own resources and will be possible only through the sympathetic help of foreign institutes and foundations, and zoological and entomological societies. We ask that anyone who can, help us. I also ask you to make the contents of my letter widely known. The zoologists at the museum are all alive and working strenuously to salvage everything worth saving."

H. F. STROHECKER

Department of Zoology
University of Miami

Points of View

A Guiding Principle for Lectotype Selection

In the unofficial version of the amended International Rules of Zoological Nomenclature issued by the Society of Systematic Zoology it is stated in paragraph 221 that "when a nominal species originally possesses a holotype . . . any other specimens are associated with it only subjectively." It should be evident, however, that a more than subjective association links a series of insects reared from a single egg-mass, or derived from a parthenogenetic stem-mother, and this relationship cannot be altered by the mere procedure of selecting one specimen as a holotype. I suggest that the words "unless acceptable proof to the contrary is available" be added to this paragraph.

In paragraphs 227 and 228, it is laid down that "if no holotype was originally designated . . . the type specimens are all syntypes. . . . Any author may select any one of the syntypes to be the lectotype of the nominal species."

This means that the great body of classical specimens that have been used as holotypes by generations of taxonomic workers are to be stripped of their authoritativeness unless they are unique or happen to have been mentioned in print as being the only type specimen. This rule, if observed and acted upon as it stands, could lead to taxonomic chaos: no attempt is made to meet the difficulties that its application will create.

To quote one example, the prominent hemipterist W. L. Distant was in the habit of labelling one specimen when describing a new species, adding the word "type" on the label. There is no difficulty today in recognising a "Distant type" in a collection, and his types have formed a basis of countless identifications by the Imperial (later Commonwealth) Institute of Entomology and of further taxonomic work by later specialists. Yet in his great contribution to the *Fauna of British India,* after describing and figuring a new species, citing localities and often the name of a repository, Distant usually does not mention the existence of any material whatsoever. This was a common practice at the time. How, in such cases are "type specimens" or "syntypes" to be determined in an objective manner? If only one specimen has been labelled by the author in the collection, how is it to be ascertained that he saw others at the time when the description was made? Dr. W. E. China (*in litt.*) has pointed out that many of the original series in the British Museum that would have been regarded as of "syntype" or "cotype" status have already been split up, and specimens have been removed to their correct systematic position in other species or even in other genera. In such cases it is now impossible, he indicated, to reconstruct the original series.

Under the proposed Rules, a reviser is permitted to choose a lectotype only from material before the original author at the time when the original description was made. He is accordingly burdened with the task of proving that the specimen that he selects was in fact part of such material. This is not his only difficulty: as "the first such selection published establishes the lectotype," he is faced with the task of ascertaining whether any such selection has been published prior to his own. This may raise the question whether or not a certain form of words, or parenthetical reference, has constituted a lectotype designation. Problematical instances are far from rare. In his contribution to the *Rhynchota* volumes of the *Biologia Central-Americana* Distant frequently discusses his own types and those of other

workers in terms that permit their recognition from the data given. Students who care to consult this work will find examples that can be claimed to be holotype designations and lectotype designations. Who is to decide each claim? Must each claim be decided authoritatively in the negative before a reviser can choose a lectotype? And what is the fate of a lectotype if an earlier and different valid lectotype designation should be found? On all these points the Rules are silent.

A careful system has been proposed governing the selection of neotypes, a comparatively rare procedure in zoology. How much more important is it to devise an equally careful system for safeguarding the authority of thousands of traditionally accepted types!

Under the proposed rules a reviser is neither compelled nor even invited to state whether his lectotype is, or is not, the same as any specimen hitherto regarded as the type, and, if not, why he has rejected the accepted type in favour of another specimen. The object of the proposed rules is apparently to ensure that in the matter of "unpublished" types a fresh start shall be made, and that the first reviser, with undisputable original material before him, shall be free to choose as lectotype the specimen that is most suitable, in the interests of stability and universality. If this is the aim, why are not the appropriate provisions laid down? The Rules do not require, nor even recommend, that a reviser consider stability, or universality of usage, or (in contrast to the designator of neotypes) the feelings of other workers: the reviser is free to choose at whim or at random, and to withhold his reasons. It is perhaps less surprising that they ignore the ethics in the following situation: where a specimen is designated as lectotype after having been received in exchange, or as a duplicate, that specimen should be returned for deposit to the institution whence it came, in exchange for a further specimen.

It is possible to devise a regulation to meet each contingency, but a system of international rules should be simple as well as effective. The guiding principle in the selection of lectotypes might well be sought in an earlier Code: *"Thou shalt not remove thy neighbour's landmark, which they of old time have set. . . ."* Existing "undesignated" types that need to be preserved in the interests of stability surely outnumber those that it would be advisable to discard for the same reason by many thousands to one. With this in mind I suggest that the following proposal be laid down in the final version of the Rules: In any case where, prior to the date of publication of the definitive edition of the amended Rules, a specimen has been distinctly labelled to distinguish it from all others with the apparent purpose of making it the paramount example of the species, it must be selected as the lectotype, if designation of a lectotype should be necessary. Furthermore, the selection of any specimen other than this is permissible only where the reviser brings forward evidence to show that the prescribed choice would be contrary to the interests of stability and universality of usage and that his proposed choice would conform appreciably better with those interests. If a reviser should follow the latter course, his designation should be subject to protest within five years after publication, after which, in the absence of protest, it could be regarded as confirmed.

The advantages of the proposal made above are, firstly, that it would leave the reviser quite free, while making him answerable in detail for any "unorthodox" designation; and secondly, that it would obviate all question of challengeable "syntypes" and debatable earlier lectotype designations, and would accordingly save the reviser a great deal of time-consuming bibliographic research. Lastly, and above all these, it would uphold the authority of existing undesignated types and stabilize usage, between the present day and the time, probably more than a century hence, when present "undesignated" types will have acquired the formal authority of lectotypes.

R. G. FENNAH
Imperial College of Tropical Agriculture
St. Augustine, Trinidad, B. W. I.

More on Margaritiferidae

In a recent issue of SYSTEMATIC ZOOLOGY (Volume *5*, pp. 141–142) there is an article by Mr. Donald F. McMichael on the petition by Mr. A. E. Ellis for the preservation of the family name Margaritiferidae Haas 1940. I agree with Mr. McMichael that this would be an undesirable step for the International Commission on Zoological Nomenclature to take, but I find myself in complete disagreement with him on every other point, especially the alternative course which he recommends in order to resolve this difficulty.

In the first place, it must be remembered that the purpose of authority citations is, not to honor any scholar who has made a significant or important contribution to our knowledge of the group to which he has given a name, but to give a clue to subsequent scholars as to where he may find the original use of the name. This is particularly true in the case of names which happen to be homonyms. In this case the name Margaritiferidae is not a homonym, but the name of the genus upon which it is based and from which is derived, *Margaritifera,* is a homonym, as I shall show later. The student who wishes to find where the name Margaritiferidae was first published, and seeing it credited to Ortmann, would naturally not think of looking through Haas' work to find it until after making a vain search through the writings of Ortmann; a search which may well exhaust his patience.

Actually the simplest way for the Commission to rectify the situation would be for the Commission to suppress the name *Margaritifera* Schumacher 1816 altogether, and to validate *Margaritana* Schumacher 1817. The earlier of these names is objectionable because for nearly a century it had been used for an entirely different genus, now known as *Pinctada* (Röding in) Bolten 1798. It is true that none of these usages complies with the requirements of the present code of rules, but that fact does not make it any the less confusing when one name is used with two widely different significations. It must also be remembered that the rules were not in existence when Woodward, Browne, Humphrey, and Megerle wrote, and no doubt their usage was considered quite correct at the time they used the name *Margaritifera.* Apparently Schumacher himself thought so. Presumably this is why he proposed the new name *Margaritana* only one year after he had published *Margaritifera.*

From 1817 until 1925 the name *Margaritana* was in universal use for this genus. The name *Margaritifera* was not forgotten, however, for during this interval it was used by H. and A. Adams, Harris, Jameson, and Michimoto in its original sense for the genus now called *Pinctada.*

Then in 1925 Kennard, Salisbury, and Woodward discovered Schumacher's use of the name in 1916 which they sought to restore. Almost immediately Henderson (1928), while admitting the justice of this claim under the rules, wrote "This seems to be an instance justifying the committee on zoological nomenclature in exercising its discretionary power by validating the name *Margaritana.*" Whether Henderson ever submitted such an application to the commission I do not know; if he did it became lost during the inactivity of the commission before it was reactivated by Mr. Hemming. At the time I was under the impression that he had done so, or I would have done so myself.

Since Mr. Ellis' application was published in the *Bulletin of Zoological Nomenclature,* several comments upon it have appeared. Dr. Henning Lemche has urged the validation of *Unio* and *Lymnaea,* but not of *Margaritifera,* which he ignored; Dr. Altena has urged the validation of *Unio* but has expressed no opinion as to *Lymnaea* or *Margaritifera;* Dr. Baker has observed, "*Margaritana* has been used more than *Margaritifera,* but either would be acceptable."

In addition to the arguments set out hereinabove there are two other objections to the use of *Margaritifera.* The first

is that it is not a noun but an adjective, and generic names should be nouns. The second is that the name proposed by Schumacher in 1816 actually was not *Margaritifera* but *Margartifera*. This misspelling may have been a typographical error, but there is no evidence in the original publication to show that it was, and emendations of supposed errors can be made under the rules only when evidence of error occurs in the original publication. If the Commission wishes to validate *Margaritifera* under the rules it must date this name from 1925 when it was first published, suppressing both of Schumacher's publications; if it wishes to validate *Margaritifera* as of Schumacher 1816 it must suspend the rules, and if the rules are to be suspended they might better be suspended in favor of the more desirable name.

To return to the family name Margaritanidae: This name was not only used by Ortmann, but also by Hannibal, Simpson, Walker, and Frierson. Hannibal's work is of no particular value, but the other four were the world's leading authorities on this group and the name which they used should be preserved, as it has gained recognition through the weight of authority.

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JOSHUA L. BAILY, JR.
4435 Ampudia St.
San Diego 3, Calif.

A Protest Against the Atomizing of Genera, with Special Reference to the Hepialidae (Lepidoptera)

There are few families in Lepidoptera which of recent years have been so rapidly enriched by the erection of new genera as the primitive group of Ghost Moths (Hepialidae). Thus Viette alone described, in the period 1948–1952, nearly 30 new genera (some of which he indicated originally as subgenera). How is one to explain this unusual increase? On one hand, we may admit that the Hepialidae had been less studied, a negligence which is typical of the interest of the majority of entomologists for some groups like the "micro's" among the Lepidoptera. On the other hand, we must emphasize the role of the modern strict specialization which eventually and almost indirectly leads to an excessive splitting up or pulverization of certain taxa. Already in 1929, the well-known zoological authority, the late Professor Handlirsch, warned all colleagues not to split individual genera and other taxa unnecessarily, as sufficient reasons to do so are not present in all cases.

> Gewiss wird es bei fortschreitender Erforschung, zumal bei wachsender Artenzahl, immer wieder nötig werden, manche Untergattungen zu Gattungen aufsteigen zu lassen. Aber die Zerfaserung, die in manchen Abteilungen des Tierreichs fast jede Art zu einer selbstständigen Gattung machen möchte, bringt der Wissenschaft nur Nachteile. Indem man dadurch den Gattungs-Namen zu einer blossen Vorsilbe des Art-Namens entwertet, gibt man, trotz dem Gebrauch zweier (nunmehr unnötigen!) Namen die Errungenschaften von LINNAEUS' Binärer Nomenklatur unbewusst wieder auf und sinkt sogar noch unter den Zustand von 1758 zurück. Man verzichtet auf die Erfassung der morphologischen Hierarchie und damit der Phylogenie. (Richter, 1948, p. 99)

If we search for some direct motives influencing the unnecessary splitting of the known genera and making a number of new ones from them, we find that one reason is an overrating of the importance of the genital armature as a taxonomic criterion. Eltringham (1922) rightly wrote: ". . . the structure of the male armature is rarely to be relied on as an indication of more than specific affinity." This is also the view of Ford (1947) and some other zoologists. Naturally, the view must not be limited merely to the male armature and likewise the female armature cannot be regarded as an indication of more than specific affinity. Now, similar trends to atomize the genera on the basis of different characters of the genitalia only are evident also among the Hepialidae (see Paclt, 1953). This has resulted in a considerable increase of the genera described in that primitive family. One cannot be surprised under such circumstances when Janse (1942) wished to solve the problem of the generic synonymy between the hepialids *Leto* Hb. and *Zelotypia* Scott solely on the basis of a study of the genitalia. A specialist once wrote (*in litteris*), "Les genitalia sont les seules choses qui renseignent bien chez les *Hepialidae*."

I have already synonymized (Paclt, 1953) a number of "new" genera of Hepialidae which have been erected unnecessarily in recent years. Since that time it may be noted that certain authors have continued to pulverize the genera already established. Thus, the neotropic genus *Aepytus* H.-S. has now been atomized into 11 poorly defined genera, of which *Gymelloxes* Viette (1952*a*), *Pfitzneriana* Viette (1952*a*), and *Aplatissa* Viette (1953*a*) should be mentioned here in addition to the synonyms of that genus as listed in my paper of 1953. Moreover, a lack of differential diagnoses, even for the genera which have been erected on sufficient grounds, is often observed in recent descriptions by certain authors who are inclined to atomize the taxa. In the Hepialidae, *Puermytrans* Viette is not compared with *Phassodes* Beth.-Bak., *Procharagia* Viette with *Hepialus* Fabr.[1]), *Lamelliformia* Viette (1951*b*, *c*) with

[1] *Hepialus* Fabr.: type *humuli* L., fixed by Latreille, 1810, Consid. gén. p. 441; cf. Viette, 1952*b*.

Cibyra Walk., *Paragorgopis* Viette (1951*c*) with *Eudalaca* Viette, *Zauxieus* Viette (1952*c*) [to which *Theaxieus* Viette (1952*c*) is clearly a synonym] with *Neohepialiscus* Viette. The generic affinity of *Pfitzneriella* Viette remains a problematic one, too.

In order to illustrate the untenability of the method employed by some authors like Viette, we may survey two genera described quite recently in the family Hepialidae.

1. The case of *Xhoaphryx* Viette (1953*b*). This genus is said to differ from *Hepialiscus* Hmps. only in some characters of the male armature. These structural differences are here less prominent than they are in the various species of the most homogeneous genera such as *Triodia* Hb. The reader may, for example, be referred to the descriptions of the genitalia of *Triodia sylvina* (L.), *T. laeta* (Stgr.) and *T. amasinus* H.-S.[2] The differences existing between *Xhoaphryx leméei* Viette and *Hepialiscus nepalensis* Hmps. indicate merely two different species (not genera) of a close biotaxonomic affinity (so far as is known). Thus the generic name *Xhoaphryx* Viette (genotype: *leméei*) becomes a synonym of *Hepialiscus* Hmps. (genotype: *nepalensis*).

2. The case of *Toenga* Tindale (1954). Although closely related to *Bordaja* Tindale, the genus *Toenga* forms a true taxon consisting of a very interesting element from Rarotonga in the Pacific Islands. The original diagnosis is based rationally on other criteria than those of the structure of the genitalia, and makes it possible to distinguish that genus from all other genera. Indeed, the descriptions of various genera of the Hepialidae, as given by Tindale (1932–1942, 1954) should serve as a standard to be followed by future authors interested in that group of moths.

[2] See: *Rév. franç. Lépidoptérol., 12*, p. 85, pl. 1 (1949); *Faune de France, 49*, fig. 54 (1948).

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JIŘÍ PACLT

Faunistic Laboratory
Slovak Academy of Sciences
Bratislava, Czechoslovakia

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